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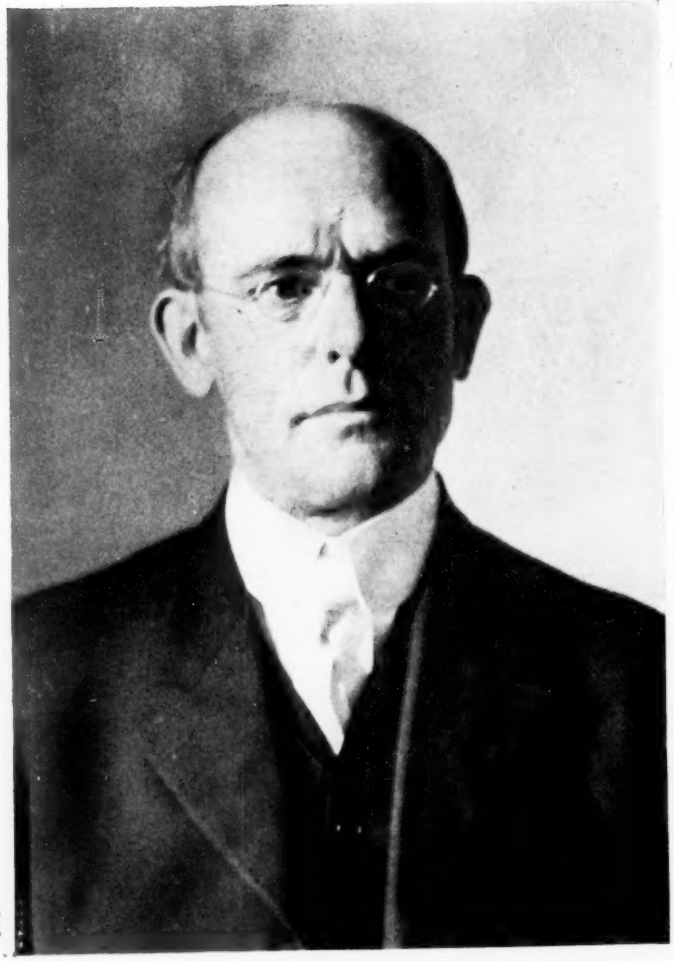

Samuel McCutchen Bain

PHYTOPATHOLOGY

VOLUME X NUMBER 4

APRIL 1920

SAMUEL McCUTCHEN BAIN

S. H. Essary

With Portrait Plate X

Samuel McCutchen Bain was born at Eagleville, Rutherford County, Tennessee, January 14, 1869, and died at Knoxville, Tennessee, January 30, 1919. He was reared on a farm and educated in the public and private schools of his neighborhood. He received the equivalent of a classical college course in Eagleville School, but his scientific education was obtained for the most part by independent study. He studied French and German under the instruction of Miss Evelyn Franklin, whom he married at Henderson, Tennessee, June 6, 1891.

Early in life he developed a love for the sciences, especially for botany. With the few books he had at his command, he commenced the study of the flora of his neighborhood. Before his graduation, he was asked to give courses in the sciences in Eagleville School, where he showed great proficiency and ingenuity in the construction and handling of apparatus in teaching chemistry and physics. In 1890 he was called to Union University at Jackson, Tennessee, to assist in the teaching of sciences and French. He soon took up the study of the flora of that section and the collecting of material for his "Plantae Tennessei Occidentalis." During a vacation in 1892, he took a portion of his collection to the University of Tennessee to compare it with the specimens in the University herbarium. Doctor F. Lamson-Scribner, who was at that time Professor of Botany in the University, was greatly impressed with his work, and asked him to return the following year (1893) as his assistant. A short time later Doctor Scribner left the University, and Professor Bain was made Instructor in Botany and Geology and Assistant Botanist in the Agricultural Experiment Station. He was advanced in position gradually and was made Professor of Botany in the University and Botanist in the Station in 1901. He continued his studies of the flora of the state, and added very materially to the University herbarium. In his Experiment

Station work he soon became interested in the preparation and use of fungicides. After several years of intense study and experimenting, he published in 1902 his bulletin on "The Action of Copper on Leaves," which gained for him wide notice among the agricultural workers of America and Europe.

In 1904 he was appointed Special Agent and Collaborator in Cotton Breeding Experiments in the boll weevil investigations of the U. S. Department of Agriculture. He devoted one-half his time to this work for a number of years, working in West Tennessee, Arkansas, and Texas. While he was actively engaged in this work, he brought out the well known "Trice Cotton," which is now grown very extensively in the South. He spent more than a year in studying the oil content of cotton seed, the results of which have never been published.

About the time of his appointment in the U. S. Department of Agriculture, he became interested in the selection of plants resistant to disease. He selected and propagated a strain of red clover resistant to anthracnose, a disease which had well nigh put an end to the growing of red clover in the State. This selection work had much to do with restoring the growing of red clover in Tennessee. He soon started on a comprehensive scale the selection of other crop plants resistant to specific diseases, but this work was greatly hindered by illness during the latter years of his life. Several projects along this line were unfinished at the time of his death.

Professor Bain was as successful a teacher as an investigator. He never sought after large classes; but he had the ability to draw about him a small band of deeply interested students, who were inspired by his earnestness and devotion to his subject, as well as by his cheerful and lovable disposition. No teacher ever had more loyal pupils. He believed in teaching Botany as a pure science, believing that the practical application of the subject would take care of itself. As he had never had a teacher of Botany himself, he developed his own peculiar methods of presenting the subject. Through his wide study and his own researches, he was able to give his students instructions fully up to the standards set by other institutions. Many of his pupils have been called to teaching and station positions in other institutions. He published a number of papers on botanical subjects, and there are several unfinished manuscripts among his files. Some years ago, he began a paper, "Southern Contributions to Natural History," which was never finished. He left a valuable collection of pictures of the plants of the Tennessee mountains, among which are a number of color photographs unexcelled for their beauty. He was a pioneer in the development and application of the autochrome process of color photography in this country.

As a man, Professor Bain was noted for his unfailing good humor and optimism. He was under all conditions polite, genial, kind, and good-natured. Even during the years of his ill health, he never lost the spirit of good cheer. He was always ready to offer council, and not afraid to ask advice of others. My personal recollections of him are very vivid. His teaching was mostly out of doors, in the woods and fields. He took his classes on many long trips around the country. During the long summer vacations, he spent his whole time collecting and studying the flora of West Tennessee.

Professor Bain was a Fellow of the American Association for the Advancement of Science, a member of the Association Internationale des Botanistes, (1900); Member auxiliare (1902), Associé libre (1912) de l'Academie Internationale de Geographie Botanique; member of the St. Louis Academy of Sciences; member Royal Society of Arts, (1911); Member Botanical Society of America; charter member of the American Phytopathological Society; charter member Tennessee Academy of Science, (1912), and President of same in 1916.

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A COÖRDINATION OF OUR KNOWLEDGE OF INSECT TRANSMISSION IN PLANT AND ANIMAL DISEASES

FREDERICK V. RAND AND W. DWIGHT PIERCE

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FOREWORD

During the past few years the question of disease transmission by insects has assumed such gigantic proportions that it has seemed advisable to canvass the whole subject in a more or less general manner in order to determine whether certain principles may not be found applicable to insect transmission of both plant and animal diseases.

The literature of human and animal pathology is now full of examples of insect transmission of disease; and following the early work of Merton B. Waite (158, 1892) and Erwin F. Smith (125, 1896) the attention of plant pathologists has been more and more directed toward this phase of the subject. As a matter of fact, the whole question of insect transmission of disease may be stated in such a way as to cover both the plant and animal kingdoms in one statement. However, since this paper is written primarily in the interests of plant pathologists, only sufficient examples will be given among animal diseases to show the distinct correlation of insect transmission in these two branches of pathology.

GENERAL RELATIONS OF INSECTS TO PARASITIC DISEASES

There are many conditions of disturbed function or anatomy caused directly by insects or other small animals without the intervention of parasitic microörganisms. Such, for instance, are the local irritations resulting from the bite of the tick, flea, spider, or mosquito, and the various dermatoses caused by lice, chigoe, red bug, and mites, among animals; and the various forms of erinose and stigmonose, and many insect galls, among plants. Some of these conditions may as truly be included under the heading of disease as disturbances caused by microörganisms, but they scarcely come within the scope of the present paper.

Setting aside, then, such cases of disease as are of direct insect causation, there are three general relations which an insect may bear toward diseases due to microörganisms. The infective principle (1) may be picked up by the insect on external parts of its body, such as the legs or outer mouth parts, where it may retain its virulence for a certain period of time.

In these cases the organism may be (a) directly inoculated, as into wounds made by the insect carrier, or (b) accidentally sown from its body under such conditions that infection follows. Such purely mechanical dissemination may be the means of spreading infection over a wide territory.

Again, (2) an insect without itself carrying infection, may cause wounds through which parasitic microörganisms find easy access into the plant or animal body, brought there by other agencies.

Furthermore, (3) microörganisms are often taken up by an insect during the feeding process and passed along unharmed through the alimentary tract. If the infective principle (a) is merely taken into the body of the insect, and, without change or multiplication, passed out in a normal way, this mode of dissemination may be spoken of as *mechanical internal transmission.* If, however, the infective principle (b) develops or multiplies within the insect body, or by its own movement goes counter to the usual course of substances through the body and finally arrives at a point from which it may be successfully transferred to its alternate host, the mode of dissemination is designated as *biological internal transmission.*

An insect may transmit a parasite to susceptible parts of the host without wounding it, and this may be done either by external, or by internal (mechanical or biological) carriage, or by both. In other cases it may also directly introduce the same parasite into wounds which it makes, and here again the infection may be carried either mechanically or biologically. With respect to the same disease there may be still other cases where individual insects, which are in no sense carriers, make wounds through which the parasite already present or subsequently present is introduced. In other words there is more or less overlapping of the different forms of insect transmission, but since the extremes are clear and definite and since one form of transmission or another generally predominates, this classification serves a useful purpose, and so far as the data at hand warrant, it will be followed in the present paper.

EXTERNAL TRANSMISSION OF PARASITIC MICROORGANISMS

External dissemination and direct inoculation by the insect carrier

Mechanical external carriage and inoculation of pathogenic microörganisms by insects is very common among both plant and animal diseases. By way of example among diseases of vertebrates it may be stated that some of the parasitic trypanosomes are mechanically carried in or on the probosces of blood-sucking insects after they have taken blood from an infected animal. When these insects feed a second time the trypanosomes pass directly into the vertebrate host, without having undergone any further change or development (cf. also p. 214).

Bacterial diseases. Among plants fire blight of pomaceous fruit trees caused by *Bacillus amylovorus* (Burrill) Trev. is the first disease of microbic origin shown by definite and extensive experimental evidence to be directly disseminated by insects. For the most part this disease is carried and definitely inoculated either into the fluid on the susceptible nectar discs or into wounds made by the insect carriers. Forbes in 1884 (45, p. 150) had suggested that probably tarnished plant bugs were often active agents in conveying the "virus" of the blight from tree to tree by inoculation with the infected sap. At this time, however, the question of insect transmission in diseases of both plants and animals was a rather moot point, and such speculative suggestions pro and con were the order of the day. It remained for the epoch-making studies of Waite (158–162, 1892–1906) to actually demonstrate the dependence of a plant disease on insect dissemination. He proved experimentally (158, 1892) that the bacillus of fire blight is carried from flower to flower by bees and other insects visiting the blossoms for pollen and nectar, and that the bacilli are present and multiply in the nectar after insect visits and that blossom blight is contracted in this manner and only in this manner. Later (159, p. 298, 1896) he states that the warm, moist weather which brings out the blossoms is particularly favorable to the development of the blight and that the bacteria-laden gum from "hold-over" cankers is then exuded copiously. Bees, wasps, and flies are attracted to this ooze and undoubtedly first carry the microbes to the blossoms in this manner. From these first infected flowers the disease spreads with great rapidity. It is almost certain also, he says, that after the blooming period insects carry the blight to the young, growing tips. The germs on the new growth of the season first appear on the nectar discs (160, 1898), where they live and multiply, and they can enter the host at this point without puncture or other injury. In 1902 (161) he stated, "We have scarcely been able to find a direct normal method of introduction of the disease to twigs without the introduction of some mechanical or insect puncture." Waite observed upwards of 40 species of insects visiting pear blossoms, and many of them were demonstrated experimentally to be carriers. The honey bee was shown to be most important in spreading the blossom blight. In different parts of the United States *Bacillus amylovorus* (Bur.) Trev. was repeatedly isolated from the mouth parts of this insect. Again and again the blight was inoculated inside of bags and kept in, and outside of bags and kept out. The direct insect relation was clearly established. It was found that insects not only distribute the blight but are active agents in puncturing the germs into the tissues (162, p. 143, 1906).

Following this pioneer work of Waite many investigators have reported upon various phases of the blight-insect relation; and up to the present

time more investigators have worked upon the insect dissemination of this blight than upon that of any other plant disease. In 1909 Whetzel and Stewart (168, p. 39) concluded on observational evidence that aphids and leaf-hoppers are largely responsible for introducing the germ into the tips of growing shoots, while these insects, together with the curculio, frequently infect wounds which they make in the fruit. In the pear orchard they found the disease seldom appearing until the trees begin to bear, that is, until blossoms are present for inoculation by insects. According to the observations and experimental evidence in one locality given by D. H. Jones in 1909 and 1910 (68–69) it appeared that a large proportion of the new twig and water-sprout infections, and practically all that occurred after the blooming period, was due to dissemination and inoculation of the blight bacillus by aphids, chiefly of the two species *Aphis mali* Fitch and *Schizoneura lanigera* Hausm. Aphids were also found to be the principal means of spreading the disease in apple nurseries, and control of the aphids reduced the number of blight infections. D. H. Jones also traced many cases of blight in pear trees to wounds due to the bark-borer (*Scoiytus rugulosus* Ratz.) and obtained cultures of the blight bacillus from several of these beetles taken from diseased pear trees. These beetles were also found in apparently healthy bark which later developed the blight around the vicinity of their borings. In 1911 (70–71) Jones gave further circumstantial evidence and finally by direct experiment proved that this beetle carries and inoculates the fire-blight germ. V. B. Stewart in 1913 (143–144) observed that fire blight is spread by aphids in quince nurseries, and showed by direct greenhouse experiments that infections occur through aphid punctures in young, succulent tissues. However, in the region under his observation, he found the tarnished plant bug (*Lygus pratensis* L.) to be much more important in the dissemination of the blight germ in nursery stock. By direct experiment he showed that these insects visit blighted tissues, become smeared with the gummy exudate, carry the bacteria to the tender growing tips, and inoculate the host tissues while sucking up the sap, with the result that the twigs soon develop typical blight. Referring to the collar-blight form of the disease on apple trees, C. R. Orton and Adams in 1914 (100) remark that "the apple-tree borer is probably the most active agent in the spread of the causal organism," and later (101, 1915) they found that in 90 per cent of the observations on collar blight, apple-tree borers had been associated with the disease at the collar. Whether this insect was a direct carrier or only provided points of entry for the blight germ was not determined. However, on account of the almost universal presence of wooly aphis (*Schizoneura lanigera* Hausm.) in collar-blight cases in Pennsylvania, it was thought possible that the aphis might be a carrier to the wounds made by borers. These

aphids congregate wherever exudations of sap occur. In explanation of an unusual outbreak of apple blossom-blight, Reed, in 1914 (111), attributed the large numbers of insects, particularly honey bees, during the blooming period to the preceding mild winter and late spring. He considered this particular epidemic as due to the concomitance of large numbers of blossoms, insects and hold-over cankers. Stewart and Leonard in 1915 (145) proved by direct experiment on apple seedlings that four sucking insects (*Campylomma verbasci* Herrich-Schaeffer, *Orthotylus flavosparsus* Sahlberg, *Poeciloscytus basalis* Reuter, and *Adelphocoris rapidus* Say.) are capable of disseminating and inoculating the blight germ. These authors consider the tarnished plant bug (*Lygus pratensis* L.) and *Campylomma verbasci* particularly important because of their abundance in nurseries and because they attack chiefly the tips of shoots where conditions are best for infection. The apple red bugs and the false tarnished plant bug are also given on circumstantial evidence as probable disseminators. In Wisconsin, A. C. Burrill experimentally demonstrated (22, 1915) that aphids (*Aphis avenae* Fab.) and leafhoppers (*Empoasca mali* Le Baron) carry infection and inoculate it into the wild crabapple (*Pyrus coronaria* L.). As a result of preliminary studies, Heald (57, 1915) concludes that leaf invasions by *Bacillus amylovorus* through water pores or stomata may in some cases be of common occurrence. (Up to this time the general supposition, based upon much careful work, had been that with the exception of the nectary infections, mechanical injuries of some sort were necessary for entrance of the organism. If this method of infection is of general occurrence and if it is shown that the germ can work its way from leaf to twig, the control of the disease will be greatly complicated.) Gossard (51), and Gossard and Walton (52) in 1916 showed experimentally that *Bacillus amylovorus* may remain viable for several days in honey and in the honey dew of aphids. These facts increase the sources of possible insect contamination. In further insect experiments (1916) Stewart and Leonard (146) found that the apple leafhopper (*Empoasca mali* Le Baron) and a capsid (*Plagiognathus politus* Uhler) gave infections, while two species of fly (*Pollenia rudis* Fabricus, and *Sapromyza bispina* Loew) and the common pear psylla (*Psylla pyricola* Förster) gave negative results. They state that possibly flies may carry infection to blossoms and wounds, but on account of their method of feeding they think it is unlikely that these insects inoculate the bacillus directly into twigs. Merrill observed a direct relation between aphid infestation and amount of fireblight infection (90, 1915) and later (91, 1917) demonstrated that aphids as readily deposit their eggs in blight cankers as in other rough places in the bark, and soon after hatching from the eggs in spring they crawl through the blight exudates. He also obtained infections by caging contaminated aphids on apple twigs (cf. p. 200).

In 1896 Erwin F. Smith (125, p. 22) experimentally transmitted the bacterial *wilt of solanaceous plants* caused by *Bacterium solanacearum* Sm. using the Colorado potato beetle, *Leptinotarsa decemlineata* Say (formerly *Doryphora decemlineata* Say), previously fed upon diseased shoots.

In the year following (126, p. 409, 1897) E. F. Smith reports infection of cabbages with the black rot organism, *Bacterium campestre* (Pam.) Erw. Sm., by means of larvae of the American cabbage worm, *Autographa brassicae* Riley (formerly *Plusia brassicae* Riley), previously fed upon diseased plants. He also considered it almost certain that the disease may be transmitted by various bugs, beetles, and insect larvae that feed on cruciferous plants. Water-pore infections were later (126, 1897; 128; 129, v. 2, p. 306, 1911) found to offer the usual mode of entrance for the bacteria into the host tissues, but it was shown experimentally that infections also occur through the gnawings of insects and slugs, and that these small animals may be the means of spreading infection to the water pores. Substantially these results were confirmed by Russell and Harding in Wisconsin (114, 1898). Brenner in 1904 (19) confirmed the results of Smith and of Russell and demonstrated that aphids also successfully disseminate and inoculate the black rot bacteria into the host. He found that a single plant louse was sufficient to transmit the disease.

The experiments by Manns (83, p. 111, 116, 1909) show that a bacterial *blade blight of oats* is distributed and inoculated by two species of aphids, *Macrosiphum granaria* Buck, and *Syphocoryne avenae* Fabr.

Burger (21, 1914), working with a bacterial rot of lettuce, found large numbers of reddish-brown aphids present in infected fields, and showed by careful experiments that these insects could distribute and inoculate the disease.

Fungous diseases. Sturgis (150, p. 191, 1898) reports a direct relation between bees and primary pod infections with lima-bean mildew, caused by *Phytophthora phaseoli* Thaxt. He discusses the special adaptation of the flower for insect cross pollination, in which process the base of the ovary and the style are momentarily exposed and come in contact with the body of the bee. This insures cross pollination, but if the bee's head or abdomen has previously touched a mildewed pod, fungous infection is no less certain to follow. Young pods often show evidence that infection has already occurred before the fall of the blossoms and that it always has taken place at the extreme base or tip of the young pods. These, he says, are the exact points touched by bees in visiting the flowers.

Waite (161, 1902) thinks from extended field observations that bees are largely responsible for the rapid spread of peach and plum brown rot caused by *Sclerotinia fructigena* (Pers.) Nort. Wasps and soldier bugs and several other puncturing insects are also concerned in making openings

in sound fruit. Bees rapidly follow in the punctures made by other insects, and in California during June and July hundreds and thousands of bees may be seen swarming over the early ripening peaches and Japanese plums. In going over decayed fruit he thinks that they carry the fungous spores into wounds made by other insects, and states that they even eat large holes in the fruit, thus probably carrying infection and also inoculating it directly into the fruit. W. M. Scott and Ayers in 1910 (119, p. 13) state that sucking insects of the squash-bug family (Coreidae) have been observed to puncture healthy and diseased fruits indiscriminately, thus not only distributing the spores but probably also inserting them into the peach. But these investigators and also Scott and Quaintance (120, p. 3–4, 1910) consider the plum curculio by far the worst offender. In the feeding and egg-laying processes the fruit is punctured and these wounds form a nidus for the brown-rot spores. This insect punctures the fruit through the coating of spray and is almost certainly also a carrier of the spores, so that the control of brown-rot is thus greatly complicated.

James Scott in 1907 (118) states that certain insects, and among them the fungus fairy fly (*Caecilius flavidus* Steph.), are to be regarded as secondary causes of the *larch canker*, since the causal fungus gains entrance through their injuries to the tender bark. Large numbers of the fairy fly and its larva, covered with spores, are found on the cankers and in the "witches brooms" and so may distribute infection to fresh districts. The tiny punctures of the larch aphid (Chermes) are also known to be a predisposing cause of this disease and should be further investigated. The following year Maxwell (88) reports that the causal fungus gains entrance through wounds, but he considers that impaired vitality from any cause has more to do with predisposition to this disease than any direct connection between aphids and infection with the causal fungus, *Dasyscypha calycina* Fckl.

The *bud-rot of carnations* was first reported by Wolcott in 1905 (170), and on account of the constant presence of mites was then attributed entirely to their injuries. In 1908 Heald (56) proved that the disease is due to the fungus, *Sporotrichum anthophilum* Peck, and from observations and experiments he considered it almost certain that the mite acts as a carrier of the fungous spores which it inoculates into buds visited for feeding purposes. Wolcott in 1908 (171, p. 31) found this mite to belong to a new species which he named *Pediculoides dianthophilus*. During the same year Stewart and Hodgkiss (142, p. 112–115) obtained substantially the same results. They add, "The fact that the disease sometimes destroys the interior of buds before they have begun to open is strong evidence that the spores are carried there by some animal and mites are the only animals found constantly in diseased buds." The mites probably visit the healthy buds to feed on floral tissues. The spores carried on their bodies germinate,

attack the interior of the buds through injuries, and later cause the decay. In the decayed tissues the mite finds a congenial breeding place from which the young later migrate to healthy buds, thus completing the cycle.

In Holland, Ritzema Bos (112, 1906), and Quanjer (105, 1907) working with *black leg* of *cabbage* (caused by *Phoma oleracea* Sacc.) showed experimentally that infection enters through wounds made by insects, particularly the cabbage maggot, *Pegomya brassicae* Bouché (formerly *Anthomyia brassicae*), and through injuries by wire worms and snails. They state that apparently all these animals also transfer the fungus from diseased to healthy plants. Manns (84–85, 1911), working in America, did not find the association of maggots and wire worms to be as important as did these European investigators. However, he considered these animals, together with the cabbage curculio, to be quite generally instrumental in to some degree aiding the fungus in its distribution and attack.

From his personal observations and correspondence with other countries relative to *Nectria ditissima* Tul., Ducloux (38, 1910) concluded that wooly aphis is in some way associated with the spread of this *apple canker*. Wiltshire, in 1914 (169) refers to the current opinion associating this insect with outbreaks of the Nectria canker, and states that Descours Desarces has proven that these insects carry the conidia on their wooly covering. Wiltshire, however, obtained negative results by inoculations made in various ways upon fresh aphis injuries. In late summer, after the bark bursts around these injuries, he thinks that entrance may possibly be afforded, and this conclusion is supported by the fact that canker attacks usually occur in the year following outbreaks of wooly aphis. Massee (87), in 1915, stated that the rapid spread of the Nectria canker coincided with the introduction and spread of the wooly aphis (*Schizoneura lanigera* Hausm.) into England. Its injuries on the branches of apple trees are exactly of the nature required by the fungus for entry into the host tissues. These insects, also, he says, carry the fungous spores.

In connection with the *pineapple fruit-rot* and *leaf-spot* caused by the fungus, *Thielaviopsis paradoxa* von Hoh, (formerly T. *ethaceticus* Went.), Larsen (75, p. 26, 1910) says that insects aid the fungus by injuring the fruit and leaf surfaces and by distributing the spores. The mealy bug (*Pseudococcus bromeliae* Bouché), and a grasshopper (*Xyphidium varipenne* Swezey) are considered most important in this connection. Of the leaf spots caused by this fungus, 75 per cent were found to have originated through grasshopper wounds. Ashby (7, 1917) considers on circumstantial evidence that the spores of this same fungus, causing one of the "leaf-bitten" diseases of pineapple, are spread by the wind, by wind-borne raindrops and by insects. He says further that the striped weevil, *Metamasius sericeus* Oliv., which is attracted to rotting patches on the heart leaves,

is an active flier and undoubtedly plays a part in disseminating the spores. (cf. p. 201).

Grossenbacher and Duggar (55, 1911), on the basis of circumstantial evidence, consider it probable that various insects, and especially a small beetle, the American currant borer (*Psenocerus supernotatus* Say.), are instrumental in spreading and inoculating the spores of *Botrysphaeria ribis* Gross. & Dug., the cause of a *cane blight of currants*.

Taubenhaus (151, 1912) considers from circumstantial evidence that aphids and red spider distribute and inoculate spores of the anthracnose of *sweet peas*.

In 1915 Nowell (95) associated the *internal disease of cotton bolls* with the attacks of certain sucking insects. This disease is characterized by a discoloration of the lint in unopened bolls without external signs of injury. In one series of observations Nowell and his associates found (a) the disease absent in the absence of the cotton stainer bug (Dysdercus spp.), (b) a high percentage of the disease where the plants were infested with this insect, (c) a constant association of cell proliferations within the diseased carpels, suggesting injury by a piercing insect, and (d), where the stain was just beginning to show, the occurrence of water-soaked spots suggesting insect punctures. Punctures with a sterile needle usually gave nothing but mechanical injury. Cage experiments with cotton stainers, on the other hand, gave a high percentage of disease, while the controls gave little or none. It was thought probable that the internal boll disease is caused by a microörganism brought in by this bug. The following year Nowell (96) discovered a specific fungus causing the disease and showed that it was carried by or followed closely upon the attacks of plant feeding bugs. In his studies of 1917 (97–98) infection was found to take place without apparent exception through bug punctures, and mainly through those made by the cotton stainer. Control measures against this insect reduced the disease to negligible proportions over large areas. In 1918 (98) several other fungi were found also capable of causing internal boll disease, and these specific fungi were isolated from the fruits of local plants belonging to seven different orders. Careful cage experiments demonstrated that the punctures of the cotton stainer, green bug (*Nezara viridula* Linn.), the leaf-footed tomato bug (*Leptoglossus balteatus* Linn.), and the red tomato bug (*Phthia picta* Drury) may all serve as channels for infection. Not a single case was found of infection other than through a bug puncture, and strong evidence was given that bugs are also the carriers. It appears that stainers carry one type of fungus and green bugs another, and this was correlated with the presence of these specific fungi on the respective preferred food plants of these two insects. The species of fungus causing the disease in any one case depended upon the preceding food plant used, but

where bugs were taken from healthy plants no infection followed. The pea chink (*Edessa meditabunda* Fabr.) always gave negative results whether previously fed upon healthy or diseased plants, (but this insect scarcely pierces the outer covering of the bolls).

Turner (157, 1918) found an association between kernel spot of pecan and the green soldier bug, *Nezara viridula* Linn. In 1916 he observed severe infestation of these green bugs in pecan groves, followed by a severe attack of kernel spot. Accordingly the following year some of these insects, collected from cowpeas, were enclosed for several weeks with pecan nuts on the trees. Examination of the nuts after they had ripened showed every one to be affected with kernel spot, while only two or three cases were found among several hundred nuts on the same tree, not confined with these insects. He had not determined upon the presence or absence of the fungus (*Coniothyrium caryogenum* R.) described by Rand in his preliminary studies upon this disease (105 a, p. 330), but he considered, in any case, that *Nezara viridula* is an important agent, either as a direct cause or as a means of dissemination.

External dissemination and accidental infection without direct inoculation

General discussion. In many other instances the relation of the insect is predominently that of a mechanical carrier only. In typical cases of this type of dissemination the infective principle is not directly inoculated into the host but accidentally sown from the insect's body, as e.g. on wounds or other portions of the host favorable for infection. This method of transmission is common in diseases of both animals and plants. In studies of human and animal diseases it has been shown repeatedly that many insects which come in contact with infected material, such as fecal matter, pick up large numbers of disease germs on their legs and bodies and carry these germs great distances, depositing them again on fecal matter, or more important still, on food or wounds or sensitive membranes. The house fly especially has been convicted of the external transmission of many species of bacteria. Most of the flies which frequent houses and food or visit man because of attraction to bodily secretions or injuries are also attracted to and breed in excreta or garbage. Hence the contamination of food by direct transportation from infected excreta is a very simple matter.

Bacterial diseases. By way of examples in animal pathology *typhoid fever* and *cholera* may be mentioned. The typhoid bacilli are often taken up from infected material by the feet or mouth parts of flies and deposited upon liquid or solid food by means of which access is easily obtained to the

human alimentary tract. Occasionally flies carry infection internally for long periods of time (cf. p. 33).

Cholera vibrios are also rather commonly disseminated by flies, particularly in those countries like India where dejecta are not properly disposed of.

Among bacterial diseases of plants, fire blight of pomaceous fruit trees is frequently contracted through various injuries to the young shoots or tender, fleshy bark. In these cases insects and birds are the agents of distribution (Waite, 160, 1898). Whetzel (166, p. 115, 1906) observed that flies constantly followed the pruner for the exuding sap and thought they might be agents in transferring the bacilli in this way from diseased to healthy trees. Hotson (62, 1916) found blight starting in hail injuries on twigs and fruit and considered the rapid spread to uninfected trees as probably due to various kinds of insects, and especially ants which he found attracted by the exuding sap (cf. p. 192).

R. E. Smith, C. O. Smith and H. J. Ramsey (134, 1912) observed flies on diseased walnuts affected with the blight organism, *Pseudomonas juglandis* Pierce, probably attracted there by the exuding organic matter mixed with bacteria. The blight organism was isolated from the bodies of such flies.

Fungous diseases. Magnus (82, p. 95, 1891) thought the teleutospores of species of Diorchidium well adapted to insect distribution because of the fact that they are sticky and are set free in dew drops or other moisture. Klebahn (73, p. 19–20, 1904) considered that insects play an important role in the distribution of *rusts* in general, and also suggested that the bright color of some species might attract insects; and Falck (42, p. 56, 1904) thought, on account of the odor frequently emanating from affected parts of the host, that the pycnospores were probably distributed by insects. Freeman in 1905 (46, p. 29) says that the early spring spores of rusts are often accompanied by structures [aecidia] exuding sweet fluids attractive to insects, which may assist in sowing the spores. Johnson (66, 1911) in his work on floret sterility of wheats in the southwest found this condition to a large extent caused by rusts. Examination of large numbers of thrips showed rust spores attached to the appendages of a considerable proportion. As the thrips were very numerous and very active, he considered that large quantities of spores must be distributed over individual plants and between fields. The prevalence of rust spores between the glumes of wheat florets and the consequent rusting of the heads was thus tentatively accounted for.

Ludwig (79, 1892) calls attention to the fact that those *smut* spores which have a roughened cell wall are found on those parts of their hosts which are regularly visited by insects, while the smooth spored sorts occur on wind

pollinated plants or on parts not regularly visited by insects. Brefeld and Falck (18, 1905) and later Jensen (65, 1918) suggest that in anther smut of plants pollinated by insects as in *Melandryum album* Garcke and *Saponaria officinalis* Linn. the smut spores are not disseminated like loose smut spores, by the wind. The flowers are visited by insects and in the case of Melandryum especially by night-flying butterflies. These insects stick their probosces into the blossoms to get honey and in this way the spores are forced out, and getting onto the insect body are said to be thus distributed to other flowers.

According to Clinton (31, 1902) insects, and especially the small pomaceous flies of the genus Drosophila, are undoubtedly one of the chief agents in the dispersal of *bitter-rot of apples* caused by *Glomerulla cingulata* (Stonem.) S. and v. Schrenk. The Drosophila flies breed abundantly in the decaying apples; and, in a damp chamber experiment, infection was carried by these flies from bitter-rot to sound apples. Thomas J. Burrill (23, 1907) thought that the spores were to some extent distributed by pomace flies but considered that no insects are largely instrumental in the distribution or development of this disease.

Cobb (33, p. 116, 1906) thinks that the pineapple disease of sugar cane caused by *Thielaviopsis paradoxa* von Hoh. (formerly *T. ethaceticus*) is often assisted in its distribution by insects, and that in all probability they are attracted by the odor. Diseased cuttings are often infested with mites and with the larvae of small beetles of the genus Carpophilus. Examination of these beetles repeatedly disclosed spores of the fungus on their bodies, and as they move from cutting to cutting, he thinks that they undoubtedly spread the disease. These beetles have a grinding crop with teeth fine enough to destroy the spores, only fragments of which were found in their intestines. Larsen (75, p. 26, 1910), working with the same fungus causing a fruit rot of pineapples, says that the fruit beetle (*Carpophilus humeralis* Fabr.) does not rupture the surface so far as could be ascertained, but that it distributes the spores from affected pineapples to newly made wounds in healthy fruits. The vinegar fly (*Drosophila ampelophila* Loew.) and other flies are also said to be important factors in distributing the spores (cf. p. 198).

That the *chestnut blight* fungus, *Endothia parasitica* (Murr.) P. J. & H. W. And., may be distributed by insects was early inferred by Murrill (94, 1906), Hodson (59, 1908), Metcalf and Collins (93, 1911), Metcalf (92, 1913), Fulton (47, 1912), and Rankin (110, 1912). Craighead, in 1912 (35) found by cultural methods that the spores of this fungus are not viable after passage through the alimentary tract of the longicorn beetle, *Leptostylus macula* Say. This result was later confirmed by Anderson and Babcock (6, 1913), but they succeeded in culturing the blight fungus in

some cases from the bodies of ants artificially contaminated or collected from pustules on the trees. Studhalter (147, 1914) by microscopical and cultural tests found twenty species of insects carrying Endothia spores on their bodies. The longicorn beetle was found to carry the largest numbers of any of the insects tested, showing that even if the spores do not survive intestinal passage through this insect it may still be a factor in the dissemination of the fungus. Later in the same year Heald and Gardner (58) showed that the pycnospores retained their viability for some time in the soil, and suggested that this offers a possible means of transport of the spores in dried mud on insects, birds, squirrels etc. Studhalter and Heald (148, 1915) found that the largest number of pycnospores were obtained from birds and insects within about two to four days after a rain. This corresponded closely with the time the largest numbers of spores were obtained from healthy bark below chestnut blight lesions. About the same time Studhalter and Ruggles (149), reviewing their experiments and observations relative to insect transmission of this disease, conclude that some insects carry a large number of spores of *Endothia parasitica* and that they are important agents in the local dissemination of the disease. This, they state, is especially true of the longicorn beetle. On the other hand, Craighead (36, 1916) suggests that in order to play an important part in dissemination, an insect must migrate from diseased to healthy trees. Most of the Coleoptera discussed by Heald and by Ruggles he says do not have this as a normal habit; the longicorn beetle never frequents healthy trees and most of the insects discussed by these authors are only occasional visitors. With respect to the chestnut blight, Craighead considers that the important role of insects consists in providing fresh wounds for the entrance of the chestnut blight fungus (cf. p. 204).

L. R. Jones, Giddings, and Lutman (72, p. 40, 1912) assert that washing and dashing about by rain is the most effective agency for local dissemination of the potato fungus, *Phytophthora infestans* (Mont.) de Bary. For longer distances wind and insects probably coöperate. Larvae of the Colorado potato beetle previously fed on blighted leaves were kept in a damp chamber over night on two healthy potato plants both of which developed the disease in six days. The mature beetles are, of course, capable of carrying the spores to greater distances and are doubtless important agents in the sowing of late blight infection in new fields

Taubenhaus (152, 1913) claims that the *black rot* of *sweet potato* caused by *Sphaeronema fimbriata* (E. & H.) Sacc. is spread in storage by means of mites and spiders. The disease followed when mites and spiders were transferred from diseased to healthy roots and pure cultures of the causal fungus were obtained when they were allowed to crawl over poured plates of solid culture media.

The same investigator (154, 1914) states that fruit flies are constantly associated with *soft rot* and *ring rot* of *sweet potatoes* in storage.

Whetzel (167, 1915) states that the spores of Botrytis blight of peony caused by *Botrytis vulgaris* Fries and *Botrytis cinerea* Pers. are produced in great quantities and are carried by wind and insects. Ants seem to carry the spores from the base of diseased stalks to the buds of healthy plants. Here in the exuded sugary solution so abundant on the unopened buds, he says, the spores find ideal conditions to germinate.

McKay and Pool (81, 1918) obtained *Cercospora beticola* Sacc. in culture from the "yellow bear" (*Diacrisia virginica* Fab.) and in one case from the greater sugar-beet leaf-beetle (*Monoxia puncticollis* Say.) but not from the sugar-beet webworm (*Loxostege sticticalis* Linn.). These insects were collected in diseased beet fields and show that the spores of this fungus may be carried on the bodies of some insects.

In work conducted at the Bureau of Entomology Field Laboratory at Thomasville, Georgia, in coöperation with the State Board of Entomology of Georgia, the late C. G. Crittenden and G. D. Smith proved that the green bug (*Nezara viridula* Linn.) after walking over a boll affected with *cotton anthracnose*, would leave a culture of the causal fungus in each foot print (Reported by Pierce).

INFECTION THROUGH INSECT WOUNDS WITHOUT DISSEMINATION BY THE WOUNDING AGENT

Many instances are on record, particularly among plant diseases, where insects are not directly concerned in transmitting the causal microörganisms, but where injuries which they initiate afford the necessary openings into the host body through which infections later take place.

Bacterial diseases. Edgerton (39, 1912), working with angular leaf-spot of cotton caused by *Bacterium malvacearum* Erw. Sm., states that there are a number of insects that puncture the bolls and thus aid the bacteria in gaining entrance. A considerable percentage of the water-soaked initial infections, especially in the older bolls, have these small punctures at the center. Faulwetter (43, 1917; 44, 1919) confirmed these observations and at the same time by cage experiments with jassids, found the part played by these insects in direct transport of the bacteria to be negligible.

In the disease of sugar-beet and nasturtium leaves caused by *Bacterium aptatum* Br. & Jam. Brown and Jamieson (20, 1913) found from inoculation experiments that infection takes place only through bruises or wounds due to insects or other mechanical causes.

Fungous diseases. Barber (13, 1901) reports that the red rot of sugar-cane caused by *Colletotrichum falcatum* Went. appears in some localities to

require a borer hole for entrance and that it usually does not spread to other parts of the cane from the joint thus entered. In other cases it is propagated by use of diseased cuttings. Lewton-Brain (78, 1908) states that the fungus is essentially a wound parasite and that a deep wound reaching the soft inner tissues is necessary for its entrance. Injuries produced by the Hawaiian sugar-cane borer (*Sphenophorus obscurus* Boisd.) are the only insect wounds in Hawaii answering this purpose, those made by leaf hoppers not being deep enough. Again, Butler (24, 1906), and Butler and Hafiz Kahn (25, 1913) claim that uninjured canes are not attacked unless the parent stem is affected. The fungus is common around injuries made by a minute borer in the midribs of the leaves, and around wounds caused by stem borers.

In discussing onion blight caused by the fungus *Peronospora schleideniana* de Bary, Whetzel (165, p. 145–146, 1904) says that leaves which have reached maturity or those weakened by breaking or by ravages of thrips seemed most easily infected by the fungus, while maggots also contribute their share in predisposing to this disease.

During experiments with biologic forms of *Erysiphe graminis* DC, Salmon (115, 1905) found that one of the brome grasses (*Bromus racemosus* L.) was immune against one form of this powdery mildew when its leaves were uninjured but became susceptible when they were punctured by aphids.

Lewton-Brain (77, 1907) speaks of the Melanconium fungus of *rind disease of sugar cane* as a wound parasite which in many cases probably enters through leafhopper punctures, but he considers the lowering of the host vitality by repeated attacks of this insect as more important in predisposing to infection. It is claimed by Cobb (34, p. 107, 1909) that entrance to this fungus is afforded through tunnels of stem borers and through punctures of leaf hoppers in the tender upper internodes.

Murrill (94, 1906) suggests that green fly and twig borer wound the tree and thus give entrance to the chestnut-blight fungus (*Endothia parasitica* (Murr.) P. J. & H. W. And. Ruggles (113, 1914) states that the making of wounds in trees, which open the way for infection, is probably the most serious part which insects have in the dissemination of this disease. Among the insects most important in making wounds are 17-year cicadas, tree hoppers, bark borers, and bast miners. A careful study of cicada wounds in eastern Pennsylvania showed 86 to 94 per cent of all infections to be in cicada stings, and observations and experiments seemed to show that the bast miner also is responsible for much of this class of infection. A later report by Studhalter and Ruggles (149, 1915) further incriminates the bast miner as an important factor in chestnut blight infection, on account of the large number of openings which it makes in the bark. Craighead (36, 1916) after a critical review of the work of Heald

and of Ruggles on insect dissemination of the chestnut bark disease, asserts that no direct insect relation has been shown to exist in this disease such as is the case in pear blight and ergot. The rôle of insects, he says, is probably insignificant in the dissemination of this disease, but their rôle in the making of wounds affording entrance to the fungus is far more important. The longhorned beetle (*Leptura nitens* Forst.), the chestnut bast-miner (*Ectoedemia phleophaga* Busck) and also three species of Sesia are mentioned as of importance in providing fresh wounds in living, healthy trees for entrance of the fungus causing chestnut bark disease (cf. p. 201).

With regard to pecan scab caused by the fungus *Fusicladium effusum* Wint., Waite (163, 1911) says: "An interesting feature was found in relation to the life history of the disease, namely, that a plant louse, which becomes common on the pecan in May, punctures the epidermis in a regular way along the veins and veinlets. The punctures of this plant louse are used as points of entrance by Fusicladium."

INTERNAL TRANSMISSION OF PARASITIC MICROÖRGANISMS

General discussion

The internal forms of disease transmission, in which the parasitic microörganisms either (1) go passively through the insect body or (2) persist and multiply within the body, present greater difficulties for study and demonstration. Furthermore the same organisms that pass through the insect's body are in a large number of instances also carried externally, showing that here, as in all phases of biological science, no hard and fast lines can be drawn. Indeed it is not only possible but probable that in many diseases where only external carriage has hitherto been proved, later researches may demonstrate that one form or the other of internal transmission also takes place.

The simplest method of internal transmission is that in which the organisms merely pass through the body of the insect in the ordinary course of food materials. There are two ways in which microörganisms may leave the body under these circumstances. Many insects are provided with a crop which serves as a storage sac, and such insects commonly regurgitate a part of the contents in order to moisten their food or sometimes as vomit after overfeeding. Ants regurgitate their food in order to feed their young. There are also certain insects that exude liquids from other parts of the body, as in the aphids where honey dew is excreted from nectar tubes. No one so far has demonstrated the liquid excreted from these nectar tubes of aphids to contain microörganisms taken up by the insect, but it is not impossible, and is a question that should be investigated. The ordinary

course, however, is for ingested materials to pass through the alimentary tract and out at the anus.

In human and animal diseases there is an abundance of evidence that disease-producing microörganisms can be taken up by an insect and regurgitated in an infective state. The house fly vomit spots have been repeatedly proved to contain infective germs even for a considerable time after ingestion.

Some remarkable facts have come to light in the study of microörganisms taken up by roaches, ants and flies. Cao (26, 1898; 27–28, 1906), an Italian investigator, has perhaps gone as far into the problem as any other one investigator, although every step has been confirmed independently by others. Working with larvae and adults of *Musca domestica* Linn., *Calliphora vomitoria* Linn., *Lucilia caesar* Linn., and *Sarcophaga carnaria* Linn., he proved that the larvae of these four species of flies when breeding in flesh may take up the germs of animal diseases as well as non-pathogenic forms; that some of these germs may pass unaltered through the alimentary tract; that some of them may remain for a long period in the intestinal canal and in a few instances may even multiply therein. Some disease germs may be taken up by the larva, persist through its metamorphosis and for days thereafter, and may be carried by the adult and deposited with its feces on food or dejecta. These bacteria were also isolated from the glutinous envelope surrounding the eggs when deposited, thus contaminating the substance on which the newly hatched larvae were later to feed.

Some bacteria have been shown to be capable of sporification as well as multiplication within the insect, and certain parasitic microörganisms have been found almost normally present in the insect body.

Mechanical internal transmission

In the mechanical internal type of insect transmission the infective principle remains viable after passage through the alimentary tract but undergoes no appreciable multiplication or development within the insect body. Only a passive relation exists here between insect and microörganism.

Bacterial diseases. *Bacillus pestis* Kit., the cause of bubonic plague, has been shown by Yersin (173, 1894) and Nuttall (99, 1897) to be capable of remaining in the intestines of flies in a virulent condition for at least forty-eight hours. Infection is usually brought about, however, through the rat flea (*Xenopsylla cheopis* Roths.), which transmits the disease from rat to rat and from rat to man. The bacilli have been found in the intestines in some cases for at least three weeks after ingestion, but it has not been demonstrated that they necessarily multiply or undergo any transforma-

tion within the insect. The bacilli are inoculated directly by the flea bite or by scratching portions of the bodies or feces of infected fleas into abrasions in the skin.

Fungous diseases. Among fungous diseases, the spores of at least seven parasitic species have been shown capable of passing through the intestinal tract in a viable condition. The fact that flies are attracted to the stink-horn fungus (*Phallus impudicus* Linn.) has long been known to botanists. T. W. Fulton (48, 1889) in his paper on the spore dispersion of Phalloids by insects, even found a reference to the attraction of flies for the sporiferous slime of this fungus in some latin verses by the old botanist, Hadrianus Junius, who died in 1575. He refers (p. 211) to other such reports by Schäffer (1760), Ventenat (1798), Greville (1826), Berkeley (1857), von Schlechtendal (1862), and Cooke (1875). The first notice of a probable adaptation to insect distribution was given by R. Standen (141) in 1879, and a fuller account (49) the following year by W. R. Gerard. All these notices, however, were more in the way of inference than of systematic investigation. Fulton attacked the problem from a scientific standpoint and demonstrated microscopically that the spores not only cling to the appendages of blow flies but pass through the body apparently unharmed. Then he sowed the sporiferous feces of flies in sterilized soil and obtained typical mycelium of the fungus, whereas in the controls none developed. He considered it probable that in the Phalloids we have a group which has become modified for dissemination by insects, and especially by those insects which habitually frequent putrid substances and would therefore deposit the spores in the most suitable nidus for their growth. It seemed probable to him also that the odor of putrescent matter in general has been developed in relation to insect visits, for the advantage to the bacteria is obvious. He suggests further that flies may not only disperse the bacteria of putrefaction but also those causing diseases such as anthrax.

Istvánffi (63, 1903) speaks of the well known spore distribution of the carrion fungi by insects, and refers to one of the stink-horn fungi, which is reported as causing a root disease of grapes in Hungary.

Cobb (33, 1906; 34, 1909) reported extensive studies of sugar-cane root rot caused by the stink-horn fungus, *Ithyphallus coralloides* Cobb, and related fungi. He proves conclusively that the spores are not only carried externally but that passage through the intestines of insects, particularly species of Sarcophagid and Muscid flies, in no way reduces their viability. The fresh fructification of Ithyphallus has a peculiar, penetrating odor that attracts insects. Flies, beetles, and ants are shown to be very fond of the sticky, dark green spore mass at the apex, and indeed flies sometimes can scarcely be driven away. There seems to be a distinct adaptation benefitting both insects and fungus. Ants take the spores to their underground

habitations, where it is fair to suppose that the spores find conditions of moisture and coolness favorable to germination. On the feet of flies spores would become widely disseminated, but by far the larger portion are swallowed and may be found in their stomachs and intestines after they have visited the sporophores. The Ithyphallus is to all intents and purposes a subterranean species, coming to the surface only a few hours for the purpose of advertising its spore product to the insect world. Its wide distribution by this means through the fields places it ever in readiness to take advantage of vulnerable points of attack in the roots of sugar cane.

Worthington Smith in 1884 (135, p. 339) and de Bary in 1887 (14, p. 227–228) noted that the glittering saccharine liquid exuded by *ergot* (caused by *Claviceps purpurea* Tulasne) is eagerly sought after by flies, and they suggest that insects aid in the propagation of this disease. Stäger (138, 1903; 139, 1910) reports a large number of insect species observed by him to visit ergot-infected grasses, and demonstrates that ergot spores are carried on their bodies. Mercier (89, 1911), however, first proved experimentally that flies (*Sciara thomae* L.) not only carry viable ergot spores on the body but also in the alimentary tract, and that they deposit these viable spores in the feces after visiting ergot on rye grass (*Lolium perenne* L.). Mercier captured other insects on diseased rye grass and showed that *Dolerus pratensis* L., *Sapromyza* sp., and *Syrphus decorus* Meig. are also capable of carrying ergot conidia in these two ways, thus completing the experimental work begun by Stäger and showing the exact method of transmission.

According to Wolf (172, 1916), the spores of *Cercospora personata* (B. and C.) Ellis, cause of *peanut leafspot*, are borne by the wind and probably also by insects such as grasshoppers. Out of a total of 75 individual insects collected in 5 different counties of Alabana, this fungus was found externally and in the feces of 54, including 4 different insect orders. Grasshoppers, katydids, and roasting-ear worms (*Heliothis obsoleta* Fab.) were among those giving positive results. The germinating power is not destroyed by passage through the alimentary tract of grasshoppers, and damage by this disease appears to be correlated with the prevalence of this insect in the fields. Grasshoppers are wide fliers and so probably distribute the spores for considerable distances.

Parrott and Fulton (102, 1914) suggested that the snowy tree cricket (*Oecanthus niveus* De Geer) is chiefly an orchard pest on account of the occurrence of cankers caused by *Leptosphaeria coniothyrium* (Fckl.) Sacc. around their oviposition wounds in the bark of apple trees. Later (1916) Gloyer and Fulton (50) in reporting their experimental studies with this disease, show experimentally that not only do tree crickets bear a wound relation to this disease, but that they actively carry the spores of the causal

fungus in a viable condition both externally and in the digestive tract and feces. The spores were carried in this manner from diseased to healthy raspberries, and from raspberries to apple trees with resulting infections. Typical cankers in apple branches were also obtained by artificial inoculation with feces of spore-fed tree crickets. It is clearly demonstrated that these insects carry the spores internally and externally and that they also inoculate them into the host. Clinton (32, 1907), in speaking of the *wilt and fruit rot of raspberry* caused by the same fungus, states that in the fruit rot phase, infection undoubtedly takes place through the flowers and very young fruit. He suggests that the fungous spores are probably carried to the blossoms by bees and other insects that have previously crawled over stems coated with the spores, but no experimental evidence is given.

The greenhouse tests of Gravatt and Marshall (53, 1917) show that the spores of the *white pine blister rust* fungus (*Cronartium ribicola* Fischer) are carried externally and in the feces of small arthropods and gasteropods and that they may remain on the body for at least a week. Germination after passage through the insect was in most cases greatly reduced but positive results were obtained from the feces of slugs, sow bugs, cockroaches, weevils and other small animals. Inoculations with the first and second pellets from a weevil gave infection on a western species of Ribes. The following year (1918) Gravatt and Posey (54) proved that gypsy moth (*Porthetria dispar* L.) larvae feed on the Peridermium stage of this fungus and carry thousands of spores on and within their bodies. As Collins has shown that these larvae may be blown as far as 20 miles, their potentiality as disseminators is obvious. That these larvae do actually transmit the disease to Ribes by the uredospores was experimentally demonstrated. Germination after passage through the insect was, however, low. Snell (136, 1919) found Cronartium spores on 40 different species of insects collected on or near white pine cankers, and quite regularly on caterpillars, stink bugs, leafhoppers, rosebugs, etc., taken on infected Ribes. The disease was experimentally induced on Ribes bushes by caging with measuring worms (Geometridae), rose beetles, larvae of a sawfly, a large spiny caterpillar, large ants, and stink bugs, showing that practically all insects that visit diseased and healthy plants may become carriers. The part played by insects confined to the pine host he says, is very limited, but their rôle in the spread of the uredo stage from bush to bush (Ribes) may be, and probably is, an important one.

According to the field observations of Martin (86, 1918) the early blight on tomatoes, caused by *Alternaria solani* (E. & M.) Jones and Grout, is distributed by flea beetles (*Epitrix cucumeris* Harris), as suggested by the fact that beetle punctures are in the centers of early blight spots. Examination of larvae and adults of the Colorado potato beetle (*Leptinotarsa*

decemlineata Say) and the tomato worm (*Protoparce carolina* L.) revealed spores of *Alternaria solani* and of the leaf blight fungus, *Septoria lycopersici* Speg. on their bodies. Excreta from these and other insects showed the presence of these spores also, and in many cases they were seen to be germinating. It was concluded by Martin that insects are important in the dissemination of these two diseases, but no direct transmission experiments are recorded.

Biological internal transmission

In the biological type of transmission the infective principle finds within the insect body conditions favorable to its development and multiplication. In this way the duration of the period of infectivity becomes greatly lengthened, and likewise the difficulties of observation and demonstration are much increased. Many of the protozoan and so-called filterable virus diseases and a few bacterial and fungous diseases have been shown capable of this prolonged existence and multiplication within the insect. It is relative to this type of insect transmission in both plant and animal diseases that some of the most careful and extended investigations have been carried out.

Bacterial diseases. *Bacillus typhosus* Zopf., *B. pestis* Kit., and *Aplanobacter anthracis* (Cohn) Erw. Sm. are sometimes capable of prolonged existence in the intestines of insects, and in some cases at least, *B. typhosus* appears to be capable of multiplication also. Faichnie (40–41, 1909) proved that flies could carry the typhoid bacillus in the intestines for sixteen days. Ledingham (76, 1911) found that the usual intestinal flora of house flies (*Musca domestica* Linn.) generally prevented successful survival of the bacillus through metamorphosis, but in some cases he was able to isolate the organism from the intestines of adult house flies which had been fed on infected material during the larval stage. (It seems evident in the case of these occasional "typhoid carriers," where infection is borne over long periods of time, that an intimate relation must exist allowing multiplication of the bacteria within the insect body.)

Among bacterial diseases of plants an insect relationship somewhat similar to the above given examples is found in *bacterial wilt of cucurbits* caused by *Bacillus tracheiphilus* Erw. Sm. It was stated by Erwin F. Smith (122–123) in 1893 that the spread of this disease is associated with the puncture or eating of the plants by insects, and in 1895 (124) (cf. also 129, v. 1, p. 92, 1905) he experimentally carried over the infection to healthy plants with bacillus-besprinkled striped cucumber beetles (*Diabrotica vittata* Fabr.) and squash bugs (*Anasa tristis* de Geer). In 1897 (127, p. 123) he asserted that in all probability the spread of this disease is almost wholly if not exclusively by insects. In his later (129,

v. 2, p. 209–298, 1911) exhaustive treatise on this disease it is repeatedly demonstrated that the striped and the 12-spotted cucumber beetles (*Diabrotica vittata*, and *D. duodecimpunctata* Oliv.) carry and inoculate the bacillus into the hosts. Experiments with squash bugs (*Anasa tristis*) fed on wilting plants under natural conditions gave negative or doubtful results. He suggests from circumstantial evidence that possibly cucumber beetles are not only agents of summer dissemination but also of winter transmission. Field cage experiments by Rand (106, 1915) in a locality free from wild cucurbits gave no infection from soil, or by flea beetles (*Epitrix cucumeris* Harr.) and aphids (*Aphis gossypii* Glov.); but gave positive and widespread infection by striped cucumber beetles in the experimental fields at large, but in cages only where these insects had been introduced. After caging with the first striped beetles to appear in spring healthy young cucumber plants gave wilt infection, starting from their gnawings. These beetles had been collected some time before wilt appeared in this locality. Later experiments by Rand and Enlows (107, 1916) abundantly confirmed the previous exhaustive studies of Smith in incriminating striped and 12-spotted cucumber beetles as direct summer carriers. All tests with aphids, flea beetles, squash lady-birds (*Epilachna borealis* Fabr.), and with seed or stomatal infection gave negative results. In these and later studies (108, 1920) a direct mathematical relation was shown to exist between prevalence of striped beetles and the spread of the wilt disease. It was also shown that insects and nematodes do not carry infection from soil to host plant, and that root infections do not occur under field conditions. Complete locality records proved that the first spring cases start on occasional plants from gnawings of cucumber beetles which in these cases must have recently emerged from hibernation. All subsequent cases developed from similar injuries, and the disease tended to spread in ever widening circles around the initial cases. It was furthermore proved that the striped beetles are sometimes capable of infecting at least 3 to 4 healthy plants successively fed upon after one initial wilt feeding, and that after one such feeding they may, in the active state, retain their infecting power for at least twenty-three days. Occasionally wilt-fed beetles retained their infective power after five or six weeks in cold storage, i.e., as long as they were able to keep them alive. Dissection and inoculation experiments from intestinal contents proved that a small percentage of both striped and 12-spotted beetles may harbor the bacillus in the alimentary tract. In a series of isolations of bacteria from the striped beetle the intestinal flora of one only out of the 10 individuals tested was found favorable to the wilt organism. In the other 9, *Bacillus tracheiphilus* was not present. Greenhouse inoculations of 10 plants from the viscera of these 10 beetles also gave 1 case of wilt. Recent studies by Rand and Cash (109, 1920)

have confirmed these results. Furthermore, they also experimentally proved that infections take place directly from beetle droppings brought into contact with freshly pierced leaf surfaces. In these cases oral contamination was prevented. In their experiments also inoculations of intestinal contents have given wilt from the first beetles to appear in the spring, and fifteen to eighteen days before field cases had appeared in the vicinity. Also *Bacillus tracheiphilus* has been isolated from the viscera of a certain percentage of wilt-fed beetles and later successfully tested on cucumber plants. From these facts it appears legitimate to conclude that this bacillus is capable of continued life and multiplication within the alimentary canal of a certain small portion of wilt-fed beetles which may be designated as "wilt carriers." There is also strong circumstantial evidence that the organism survives the winter in this manner.

Relative to the *olive-knot* organism (*Bacterium savastanoi* Erw. Sm.), Erwin Smith stated in 1908 (130, p. 42) that old tubercles are eaten by various insects, and he considered it possible that some insect carrier may play a part in the distribution of the disease. The following year Petri (104, 1909) reported his exhaustive studies on this phase of the problem and showed that a definite symbiotic relation exists between *Bacterium savastanoi* and the olive fly, *Dacus oleae* Rossi. He found bacteria constantly localized in the fourth gastric pouch of the larval midgut. The presence of these bacteria was demonstrated from the moment when the larvae emerged from the egg up to a point immediately preceding the pupal stage. The position of the bacteria in this blind sac was such that during metamorphosis they were not expelled as a whole, but as they increased enormously in numbers some of them were from time to time passed out of the anus in the ordinary course of ingested food. Neither bacteria nor other microörganisms were found in the salivary glands or the malpighian tubules of the larvae. Immediately preceding the pupal stage, the gastric pouch and all the rest of the digestive tract were almost completely emptied. A few bacteria, however, still remained near the lower aperture of the cardiac valve and they became passively transported into the esophagus, where, between the folds of the cuticle, they remained localized throughout almost the whole period of development. With the full development of the adult fly the course of the bacteria was lost for a short period of time, varying according to the season of the year. However, the bacteria appeared irregularly a little later in a glandular sac above the pharynx. Petri did not succeed in cultivating *Bacterium savastanoi* from the pharyngial sack, but yet was able to produce the tubercles in olive by inoculating its contents. After the emergence of the adult these bacteria again suddenly developed at the expense of the abundant secretions of the epithelial cells lining this gland, and from this point they rapidy dif-

fused into the midgut where they were later found in ovoidal groups. In the female the bacteria were also localized in numerous small glands near the anal opening which is situated on the ventral side of the ovipositor. The development of the bacteria appears to be independent of the amount of food taken in by the insect, but to bear a direct relation to its functional activity. Thus, in the female emerging in winter not only are the eggs very slow in forming but the bacteria in the pharyngeal gland are also slow in development. The transmission of the bacteria from the female to the egg occurs through the ejection of a small quantity of bacteria from the anus at the same time that the egg is deposited in the olive branch. Thus are these microörganisms distributed over the surface of the egg at the moment when it passes through the cloacal canal of the ovipositor. During the development of the embryo within the egg the bacteria multiply actively around the micropile in the gelatinous envelope, and later penetrate the egg by passing through the chorion and through the numerous air canals surrounding the micropile. The bacterial content of the blind gastric pouch of the larva is not a pure culture of one species of bacteria alone. However, *Bacterium savastanoi* is present on the egg and in the micropile, in the gastric pouch of the larva, in the midgut, and in the pharyngeal glands of the adult, and in the anal glands of the female. These facts were shown by direct inoculations into olive branches followed by development of typical olive-knot tubercles and isolation of the causal organism from them. In a few cases Petri also succeeded in isolating the olive-tubercle organism directly from the gastric pouch of the larva and from parts of the digestive tract of the adult, but it occurs here sparingly in comparison with saprophytes. The bacteria subsist on the glandular secretions of this insect and on the death of the host all further development of the bacteria ceases. Petri concludes that *Bacterium savastanoi*, cause of olive-knot, is the normal symbiont in the digestive tract of *Dacus oleae*, and that the yellow organism (*Ascobacterium luteum*) often associated with it in great abundance, is a follower. Horne, Parker, and Daines, (60–61, 1912), working in California, found no biting or piercing insect concerned in the dissemination of the organism there, and concluded that the distribution is adequately accounted for by the spattering of rain and the accidental tracking of birds, insects, etc.

Tonelli (155, 1913) working with a *bacteriosis of oleander*, concludes that the scale insects, *Aspidiotus hederae* Vall. (*A. nerii* Bouché) and Lecanium sp., and the mite, *Tetranychus telarius* Linn., with certainty carry infection on their mouth parts and directly inoculate it into this host. He also considers it probable that a species of Diptera frequenting the flowers may carry infection to the stigmas. Both Smith and Petri agree, however, that *Bacterium savastanoi* when inoculated into the oleander does not produce

tumors, and therefore cannot be the cause of the oleander tubercle as is claimed by Tonelli.

Johnston (67, 1912) states that the field evidence all points in the direction of insects as instrumental in disseminating *coconut bud-rot* caused by *Bacillus coli*. He isolated the bacillus from the intestines of earwigs and from the droppings of turkey buzzards; and considers it probable from his studies that insects are carriers of infection. (Forms of *Bacillus coli* have from time to time been isolated from the alimentary tracts of insects as apparently normal intestinal inhabitants. The insect relation to this disease presents an interesting problem.)

Fungous diseases. Berlese (15, 1897) has shown how some insects, particularly ants and flies, contribute to the diffusion, preservation and multiplication of certain yeasts and molds. He demonstrated that ants may carry yeasts and molds up from infected soil and successfully inoculate grapes on the vines above. Flies fed upon yeasts gave these yeasts again in cultures from the feces, while flies fed upon killed yeast cultures yielded negative results. Berlese also demonstrated that yeasts multiply within the bodies of flies, and he found the sugary solution in the crop an ideal situation for their development. As a result of these studies he considered that during the cold season some yeasts are chiefly preserved and perhaps increased within the bodies of insects.

Schneider-Orelli, in 1913 (116), found a symbiotic relation existing between the beetle, *Xyleborus pyri* Peck. (formerly *X. dispar* Fab.), and the fungus, *Monilia candida* Hartig. He demonstrated by cultural methods that the female beetle always carries in the crop a store of living fungous cells which are not used up in her metabolism. Even when kept without food for two and a half months the living fungus was still found to be present in the crop. Shortly after the boring by the female into the wood of orchard trees the passage becomes covered with a fleecy white growth of the fungus which develops inward with the extension of the passage. Under normal conditions this nutrient fungus is present in practically pure culture, but with the growth of the larvae in the passage the fungous layer disappears and at the time of hatching only the black walls of the passage are left. Schneider-Orelli concludes from his experiments that the fungus itself is not an important factor in injuring the tree, as artificial borings alone resulted in the death of young trees in the same manner as from the insect borings. Inoculations with the fungus alone caused little or no browning of the adjacent wood in healthy, growing trees.

Protozoan diseases. The relation of the various forms of human malaria to Anopheles mosquitoes is too well known to need discussion. Many other instances of biological transmission of protozoan diseases of man and animals by insects are on record. Such, for example, are the trypanosome

diseases transmitted by the tsetse fly in Africa, viz., the *sleeping sickness* of man, caused by *Trypanosoma gambiense* Dutton, and *nagana* of ruminants, caused by T. *brucii* Plimm. & Bradf.

Spiroschaudinnia duttoni Novy & Knapp, the cause of African *relapsing fever*, is taken up by the horse tick (*Ornithodorus moubata* Murray), which lives in the mud floors of huts or in the soil where caravans habitually camp. The spirochaetes have been demonstrated in the ovaries and eggs of female ticks and have been experimentally carried to the third generation, showing a true hereditary transmission. Furthermore, it is said that the bite of individual ticks may still be infective one and a half years after an initial feeding on an infected host.

There is at least one instance of a protozoan plant disease in which the parasitic organism passes one phase of its life history in an insect. It was demonstrated by Lafont (74, 1910) that *Leptomonas davidi* Lafont causes a "*flagellosis*" in the latex of several species of Euphorbia. This disease is transmitted by the bug, *Nysius euphorbiae* Horvath., which is the permanent alternate host. The genus Leptomonas is composed of protozoa which are almost exclusively insect in their origin, although some of them have been shown to be pathogenic to vertebrates.

Filterable contagium diseases.[1] Among both plants and animals the so-called filterable virus diseases are of fairly common occurrence. Some of the diseases formerly classed as "filterable virus" diseases have since been demonstrated to be due to parasitic microörganisms. In all this class of infections the method of contraction and the sequence of signs or symptoms give a "clinical picture," so to speak, of a parasitic disease. The only difference is that in the "filterable virus" diseases the causal contagium has thus far eluded our microscopical and cultural methods.

Among animal diseases of this type *yellow fever* is a well known example. This dread scourge of the tropics is borne by mosquitoes, and the ultimate contagium will pass through the pores of a Berkefeld filter. The contagium of yellow fever circulates in the blood stream of a patient for at least three days after the initial chill. To become infected a female Aedes mosquito (*Aedes calopus* Meig.) must bite a fever patient during this first three days, whereupon a latent period of twelve days must then elapse before the infected mosquito can transmit the disease. Injection of blood from a fever patient during the first three days will induce the disease in a non-immune person; otherwise the only known method of transmission is through the bite of this mosquito. (Noguchi, through a careful and ex-

[1] The term "contagium" has been suggested by Dr. H. M. Quanjer as synonymous with any *infective principle*, whether of known or unknown origin. Its use in the place of "virus" with reference to the so-called "filterable virus" disease does away with objectionable connotations, and leaves nothing to be taken back.

tended investigation, has recently shown yellow fever to be due to *Leptospira icteroides* Noguchi. This serves only to emphasize the statements made in the preceding paragraph.)

In the plant kingdom those diseases classed as "infectious mosaics and chloroses" easily fall under the heading of filterable contagia. The first of this type of plant diseases demonstrated to be transmitted by insects is "*curly leaf*" or "*curly-top*" of *sugar beets*. On circumstantial evidence E. D. Ball in 1906 (8) connected this disease with the beet leafhopper (*Eutettix tenella* Baker) as a cause. He states that the injury does not appear to be due to the amount of sap removed, but that the punctures of this insect seem to cause a thickening of the leaf veins and an unhealthy condition of the plant. He refers also to other species of this group of leafhoppers as causing somewhat similar disturbances in other plants, particularly in the common pigweed. In 1909 (9) he went over the results of his earlier work somewhat more in detail, stating that the greatest abundance of curly-leaf followed the greatest prevalence of beet leafhoppers, and that the signs of disease induced by this leafhopper are specific. In sugar beets the abnormal condition apparently spreads until the whole plant becomes involved, even though the leafhoppers have long since disappeared. The disease was found also to persist the following year in the root. Spisar (137, 1910) refers to the work of Ball but gives no new evidence. Shaw (121, July, 1910) gives the first definite experimental proof that curly-top is directly transmitted by the beet leafhopper. In 1908, at Townsend's suggestion, Shaw sent beet leafhoppers to Washington, D. C. where cage experiments demonstrated the disease to be transmitted by this insect. These cage experiments were repeated and amplified many times by Shaw in the field, and always with the result that the disease was transmitted by beet leafhoppers but not by aphids, thrips, or red spiders. The nymphs appeared more virulent than the adult leafhoppers. Curly-top beets were never found to recover but seed from such beets gave healthy progeny. It was not found possible to communicate the disease from an affected to a healthy plant except through the intermediary of a leafhopper. No outbreaks of curly-top are known outside of the native habitat of *Eutettix tenella*, and no other insect or species of leafhopper is known to induce this disease. Shaw says that an active, persistent agent is introduced by this insect, which sets up disturbances through the whole plant. R. E. Smith and Boncquet (132–133, 1915) repeated and confirmed the work of Ball and of Shaw. They further showed that one leafhopper confined upon one leaf of a sugar beet plant for five minutes was sufficient to induce the disease. They also carried over the disease by grafting a portion of a curly-top root into a healthy root. Townsend (156) in 1915 asserted that so far as determined, *Eutettix tenella* is the only carrier of curly-top, but

that there are instances where leafhopper infestation does not produce the disease even though external conditions seem favorable. He then asks this question, "Are the beets sometimes resistant or is *Futettix tenella* sometimes free from the exciting agent?" R. E. Smith and Boncquet (133, p. 340, 1915) conclude from their experiments that no more than three hours feeding is necessary for the leafhopper to obtain the pathogenic factor, but that at least 24 and not more than 48 hours must elapse after feeding before the insect can induce the disease. These facts suggested to these investigators that curly-top is not carried mechanically but that some development takes place within the body of the insect during the first few hours after feeding on a diseased plant. At the same time Boncquet and Hartung (16, 1915) report convincing experiments with *Eutettix tenella* obtained from wild plants (species of Artemisia and Atriplex) in the Tulare Lake region of California. These leafhoppers, when caged with healthy sugar beet plants, did not induce curly-top, while in control plants caged with local leafhoppers from diseased beets the disease was readily induced. After three weeks 60 of these "wild" leafhoppers were caged with curly-top beets and subsequently transferred to 60 healthy plants. Out of these 60 plants 50 developed typical curly-top while the remaining 10 were doubtful cases. This clearly demonstrates that the leafhopper is not in itself infective, but only after feeding on diseased plants. Ball, in 1917 (10) reported in detail upon his own work and that of other investigators relative to curly-top and its transmission. Boncquet and Stahl in 1917 (17) showed by experiment that beet leafhoppers previously fed upon curly-top beets could transmit the disease to mallow (*Malva parviflora* Linn.). Stahl and Carsner (140) in 1918 obtained nymphs nonvirulent as to curly-top by collecting them as they emerged from the egg and before feeding. However, after feeding on curly-top beets these same nymphs were able to transmit the disease. Finally Carsner (30), in 1919 has demonstrated by careful and detailed experiments that a number of wild plants are susceptible to the curly-top disease, that virulent leafhoppers retain their ability to infect for a long period after removal from susceptible plants (e.g., 58, and 111 days), and that at least some of the leafhoppers are infective when they enter the beet fields in spring. He asserts that there is substantial evidence that the adult leafhoppers which leave the beets in the fall are not those which appear on beets in the spring, but individuals of a new brood developed on wild vegetation. From these facts he considers there is no question as to leafhoppers retaining their virulence long enough in the fall to infect susceptible wild annuals, such as filaree (*Erodium cicutarium* (L.) L'Her.), which in California appears soon after the first fall rains. Some of the leafhoppers developing on these infected wild hosts undoubtedly secure from them the contagium to infect

young beet plants in the spring. "Thus, it seems highly probable, the overwintering of the virus is accomplished."

The connection of insects with *mosaic of tobacco* has been carefully worked out by Allard. He first noted (1, 1912) that under controlled conditions in the course of greenhouse experiments with this disease, healthy plants were always obtained when grown in screened cages frequently fumigated to prevent aphid infestation. On the other hand, when colonies of aphids present in the greenhouse were introduced into cages with healthy plants the result was a wholesale occurrence of mosaic. In 1914 (2) he reports the spread of tobacco mosaic in seed beds and fields, which was unquestionably associated with aphid infestation (*Macrosiphum tabaci* Perg.). By direct experiment (4, 1917) he then showed that the peach or spinach aphis (*Myzus persicae* Sulz.) may actively transmit the infective principle but not until after the insect has fed upon diseased plants. Tests with a large green aphis (*Macrosiphum lactucae* Kalt.) from lettuce gave negative results although they readily fed and multiplied upon diseased and healthy tobacco plants. Similarly pelargonium plant lice (*Macrosiphum pelargonii* Kalt.) failed to carry the infective principle from diseased to healthy plants. This species, however, would not feed upon tobacco and hence could not be maintained for long under the experimental conditions. Preliminary tests with white fly (*Aleyrodes vaporarium* Westw.) and with red spider (*Tetranychus telarius* Linn.) gave negative results. Allard finally observes that Preissecker in 1903 and 1905 had noted the association of tobacco mosaic with attacks of plant lice, but that it does not appear from his writings that he looked upon these insects as actual carriers of the infective principle of the disease.

Allard (1, 1914; 5, 1918) considers it very probable from his observations and experiments on mosaic of pokeweed (*Phytolacca decandra* Linn.) that this disease is also insect transmitted.

Again, (3, 1916) from circumstantial evidence together with his experimental proofs in the case of mosaic in tobacco, Allard considers it probable that *tomato mosaic* is also transmitted by aphids.

Taubenhaus (153, 1914) reports experiments with *mosaic of sweet pea* in which aphids collected both from diseased plants and from the field at large gave mosaic to healthy plants. Sweet pea plants inoculated by needle prick from diseased plants developed mosaic while those inoculated from healthy plants remained healthy.

By careful experiments Doolittle (37), and Jagger (64), working independently (1916), showed that aphids (*Aphis gossypii* Glover, used by Doolittle) collected from plants with *cucumber mosaic* transmit the disease to healthy plants, but that aphids fed upon healthy plants do not carry infection. Transmission by striped cucumber beetles was later (1918) demonstrated by Doolittle and Gilbert (37a).

Loren B. Smith (131, Feb., 1918) reported on experimental evidence that *spinach blight* is a specific communicable disease which is transmitted to healthy plants by insects. Shortly afterward McClintock and L. B. Smith (80, July, 1918) together published a detailed account of their extensive studies of this spinach disease. Healthy plants were successfully inoculated by needle pricks with the contagium from diseased plants and with the crushed juice of aphids fed upon diseased plants. The potato aphid (*Macrosiphum solanifolii* Ashmead) and the spinach aphid (*Rhopalosiphum persicae* Sulzer), free from infection at first, were demonstrated to transfer the blight to healthy spinach after feeding upon diseased plants. Control plants invariably remained healthy. Later these two species were obtained from 4 different states where spinach blight did not occur and they failed to induce the disease on healthy plants until after they had fed on blighted spinach. The same two species collected locally and tested at the same time produced the disease. It was experimentally shown that a small percentage of the offspring of aphids fed upon blighted plants, though born and reared on non-susceptible species of plants, may prove infectious to spinach. The juices of these non-susceptible plants invariably gave negative results upon inoculation into spinach. It is evident that the infective principle is capable of transmission from parent to offspring. Even after molting a "virus-bearing" aphid remains infective, showing that the contagium is carried internally. Furthermore, successful inoculations were obtained from 4 generations representing 3 strains and 2 species of aphids, after one feeding of the parents on diseased spinach. However, the incubation period of the disease is longer with the later generations. It was also demonstrated that not *all* individual aphids fed upon diseased spinach are "virus carriers." It was further proved that aphids (*Macrosiphum solanifolii*), after feeding on wild mustard, a non-susceptible plant, were still infective although neither they, nor their parents for a long time, had fed on spinach. Inoculations with the juice of mustard plants gave a negative result. These investigators demonstrated that the contagium may be carried from spring to fall by a direct line of aphids, and that non-virus bearing aphids must remain on diseased plants 5 minutes to 14 hours to become carriers. The bean aphid (*Aphis rumicis* Linn.) and tarnished plant bug (*Lygus pratensis* Linn.) gave infections after feeding on blighted spinach. Negative results were obtained, however, with the adult of the southern corn rootworm (*Diabrotica duodecimpunctata* Olivier), the green plant bug (*Nezara hilaris* Say.), *Thrips tabaci* Lind., *Smynthurus hortensis* Fitch, and *S. quadrimaculatus* Ryder. McClintock and Smith compare their findings with the results of animal disease investigations, and conclude that spinach blight, together with the "filterable virus" diseases in general, are due to ultra-microscopic organisms.

In greenhouse experiments it has recently been shown by Schultz et al (117, 1919) that potato mosaic may be transmitted to healthy plants by aphids after feeding on plants affected by the disease. Untreated plants and those treated with non-virulent aphids remained healthy. It should be added that all three groups of plants came from the same tubers, thus precluding the possibility of "seed" transmission in the positive cases recorded.

Ball has recently (11, 1919) reported a series of observations and experiments upon a potato disease which may be tentatively included here. He has clearly demonstrated its dependence upon the potato leafhopper (*Empoasca mali* LeB.), and given the name "hopperburn" to the disease. This species of leafhopper, and this species alone, is shown to cause similar signs on several hosts, while the effects of other leafhopper species on these same hosts is entirely different. Whether or not hopperburn will prove to be a specific transmissible disease like curly-top of beets remains to be demonstrated, but in any case its relation to the potato leafhopper appears to be a specific one. In a later report of the same year (12, 1919) Ball reports the recovery of a caged potato plant after the removal of the leafhoppers, while during the same time the disease continued to spread in the field at large. Furthermore, this disease does not appear to spread from one part of the plant to another as in the case of curly-leaf of beets, and it must therefore be quite different in nature.

CONCLUSION

The literature on plant diseases transmitted by insects is thus seen to be fairly extensive, and the importance of insects as disseminating agents becomes from year to year more apparent. In fact, the investigations of the past three decades have completely revolutionized our view of the rôle of insect transmission in both plant and animal diseases. However, in many cases authentic information is still lacking as to the exact methods of inoculation and transmission, and in some instances too much is left to inference and circumstantial evidence; but enough really good work has been done to show an exact correlation between the findings of plant and animal pathology. Furthermore, it is not to be doubted that future work will fill up many of the existing gaps in our knowledge and will add greatly to the list of insect borne diseases.

In many problems of insect transmission unquestionably the best results will follow a collaboration between pathologist and entomologist. In order to follow such problems to a scientific and logical conclusion a great amount of exceedingly detailed work is necessary, not only with the host plant and its parasitic microörganism, but with the disseminating agent

as well. It is necessary to know the habits and the anatomy of the insects concerned. Furthermore it is often imperative to breed uninfected insects to act as agents of transmission and as controls on an experiment. A pathologist can hardly expect to know all the technique of breeding insects any more than an entomologist can expect to know the technique of culturing microörganisms.

In any case of suspected insect transmission the first step is to determine whether the contagium is carried on the insect's body. In some diseases this may be determined microscopically. In other instances, such as the bacterial diseases, it may be necessary to culture the organism. This may be done by washing the body, or separate parts of the body, in a sterile fluid medium and subsequently plating out the organism. In all cases where possible this should eventually be done in order to determine how long the parasite retains its virulence on the body of the insect.

A second series of experiments should determine whether the parasite retains its virulence after passage through the alimentary tract of the insect. Attempts should be made to culture the organism from the intestinal contents and from the feces; and in many cases the host may be inoculated directly from these sources.

In the case of many plant-feeding insects there is a progressive movement over the host, and if the insect is in the habit of defecating at the time of feeding it is likely that the feces will be dropped sooner or later directly on an abrasion which the insect itself has made. Experiments should be devised to determine whether the dropping of contaminated feces on a fresh injury will induce the disease in the host. It is, of course, imperative to preclude the possibility of contamination from the mouth parts or other sources. In some cases insects known to be non-infective may be first used to injure the host. Furthermore, in some diseases sensitive parts of the host may become infected without the intervention of injuries of any sort.

Other internal organs of the insect, such as the salivary glands or the crop must sometimes be tested for the presence of the parasite. In many cases this will involve the devising of special dissecting and culturing methods. In all cases, so far as possible, both cultures and direct inoculations should also be made with the contents of each organ studied.

It is important to determine whether the parasite can be transmitted directly by the bite of the insect, and in the case of positive results to find whether the contamination is merely from the external mouth parts or from the salivary glands or portions of the alimentary tract. Internal oral contamination may sometimes be determined by sterilizing the external portions of the body and mouth parts and allowing the insect to feed upon the host without defecation. In other cases cultural or microscopical methods must be used.

Among the points to be studied, then, are the following: It is necessary to determine on or in what part or parts of the body the contagium is carried; whether the transmission is mechanical or biological; how soon after taking up an infective principle transmission is possible; how long the insect remains infective; whether an infected larva may retain the contagium through its metamorphosis; whether the contagium can be transmitted to the offspring, and if so, for how many generations; whether the offspring can transmit the disease at any stage of its development; whether an infected insect remains infective after a period of feeding on non-susceptible hosts; and whether the contagium winters over in the insect. The mere fact, however, that the contagium of a disease is found in or on the body of an insect should in no case be taken as final proof of an insect relation to transmission. In many diseases an inoculating needle, a piece of wood, or *anything* which happens to come into contact with the diseased tissues will carry upon it some of the contagium. *The final criterion, then, should be the actual transmission of the disease under controlled conditions simulating as nearly as possible those found in nature.*

The task of working out all these varied ramifications of the problem in the case of any specific insect transmitted disease will require a good technique and the utmost care and patience on the part of the pathologist. Much may be learned from animal pathologists and a direct collaboration with entomologists will often eliminate pitfalls and facilitate the attainment of the ultimate goal.

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THE PHYLLOSTICTA BLIGHT OF SNAPDRAGON[1]

EDWINA M. SMILEY

WITH EIGHT FIGURES IN THE TEXT

While examining benches of snapdragon in greenhouses at Batavia and Corfu, New York, in the spring of 1917, certain plants were found to be infected with a disease the symptoms of which closely resembled those of the anthracnose. On further study, these symptoms proved to be those of the Phyllosticta blight. The same disease was observed in gardens at Ithaca, New York, during the summer of 1917, and again in 1918, on both garden and greenhouse plants. As far as is known the commonly cultivated species of the snapdragon, *Antirrhinum majus* L., which has been known to gardeners for centuries, is the only host affected by this disease. All of the thirty or more varieties of the species which have come under the observation of the writer showed susceptibility to the blight, but no detailed study has been made of their relative susceptibility. It was observed, however, during the summers of 1917 and 1918, that the leaves of the red-stemmed varieties such as the Giant Garnet are severely affected, while those of the green-stemmed varieties like the Yellow (intermediate) and Silver Pink are attacked slightly or not at all. The reverse is true of the stems; lesions on the green stems are larger and more numerous than those on the red stems. These observations were made on plants which were growing in the same garden under the same conditions.

Similar observations were made in the case of artificially inoculated greenhouse plants. Infections on stems of the Giant Garnet, for example,

[1] Also presented to the Faculty of the Graduate School of Cornell University, May, 1919, as a major thesis in partial fulfillment of the requirements for the degree of Master of Arts.

After the completion of this manuscript and its presentation for publication, a paper on the same subject by E. F. Guba and P. J. Anderson appeared in Phytopathology for August, 1919. Since this work was done quite independently, the writer having no knowledge of the others' work, and the two sets of results being for the most part in agreement, it seemed best to publish this paper without change in the original manuscript.

Acknowledgement. The writer wishes to express her indebtedness for the helpful criticisms and suggestions given by Professors H. H. Whetzel and the late V. B. Stewart, under whose direction the work was conducted, and for the painstaking care of Mr. W. R. Fisher in the making of the photographs.

are secured with difficulty, while on stems of the Silver Pink, Yellow, etc., they are easily obtained. The green leaves of the latter forms are more difficult to infect than the red leaves of the first named.

THE DISEASE

The Phyllosticta blight was first described by Sydow[2] in 1899, as a spot occurring on the leaves, usually at tips or margins, of *Antirrhinum majus*

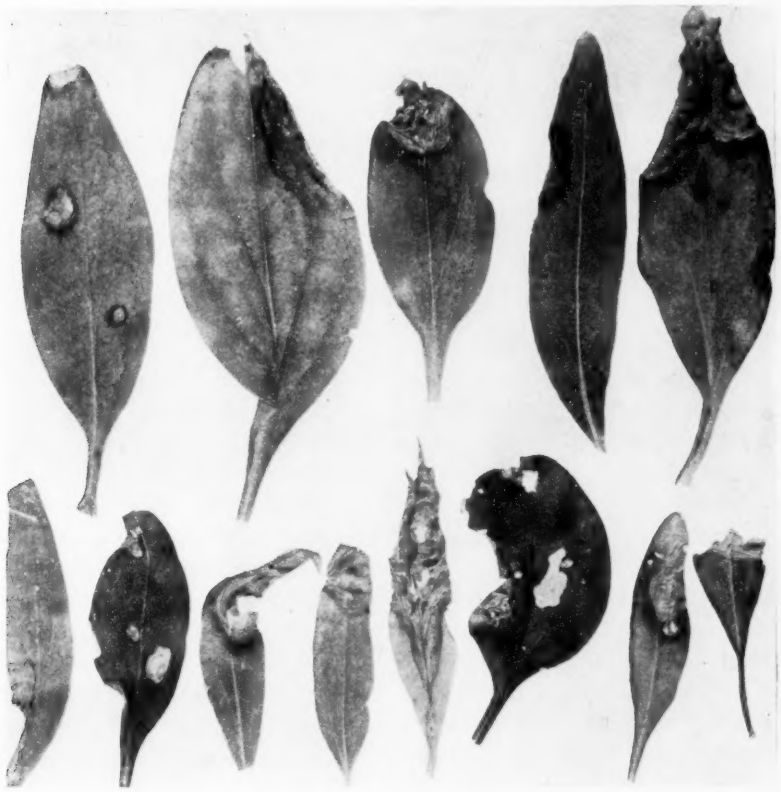

FIG. 1. SNAPDRAGON LEAVES AFFECTED WITH PHYLLOSTICTA BLIGHT
Various types of lesions and their zonate character are shown.

in Steglitz, Germany. In America it was first recorded in 1900, by Stewart,[3] who gave it the names "stem rot" and "branch blight," preferring the latter as more descriptive. Stewart, however, describes only the

[2] Sydow, P. Beiträge zur Kenntniss der Pilzflora der Mark Brandenburg II. Hedwigia **38**: Beiblatt (134). 1899.

[3] Stewart, F. C. An anthracnose and stem-rot of the cultivated snapdragon. New York (Geneva) Agr. Exp. Sta. Bul. 179: 109–110. 1900.

browning and dying of the branches, making no allusion to whitish oval spots on the stems and leaves. The disease has since been observed in Indiana and several times in Geneva, New York (F. C. Stewart, letter to writer). It has lately been reported from Massachusetts by Anderson,[4] who suggests the possibility that the diseases described by Sydow and Stewart are identical. Sydow did not mention the occurrence of the disease on the stems and, with the exception of Anderson's suggestion, no report of the relation between the stem blight and leaf spot stages, as far as is known to the writer, has been made in literature. Both forms were found on garden and greenhouse plants observed at Ithaca, New York, during the summer and fall of 1917 and 1918.

In garden plants the chief importance of the disease lies in the unsightly appearance of the spotted leaves and brown, withered shoots. In greenhouses, where the snapdragon is grown on a large scale for bedding plants or for cut flowers, the unsalable condition of the dwarfed young plants or the reduction in blossom yield due to the killing of the branches may result in considerable loss.

SYMPTOMS

The lesions appear on out-of-door plants in late June or early July. On greenhouse plants they appear in the late fall, when the seedlings or cuttings have reached a height of 6 or 8 inches. Plants of any age are susceptible, but very young seedlings are not often attacked.

On the leaves. The effects of the disease on the leaves are various (fig. 1). The first evidence of its presence is the appearance of small dark spots, brownish purple in color on the red leaves, dull greenish brown on the green leaves. These spots most frequently occur at the tip of the leaf or on the margin near the tip. Sometimes, however, lesions may occur in the lamina, in which case they are nearer the base than the tip. The spots are visible on both sides of the leaf and soon become cream-colored and slightly sunken in the center. As the lesions spread, the cream color changes to pale brown, the advancing margin remaining dark. The older lesions are distinctly zonate with fine raised ridges limiting the zones, and the upper surface is thickly dotted, especially toward the center, with small black bodies easily visible to the naked eye. If the tip of the leaf is affected, usually only the one lesion is present, but the margin of this lesion often advances downward into the blade rapidly and irregularly until more than half of the leaf is involved. If the early lesions appear in the lamina, one or several may occur. These spots are elliptical, though the

[4] Anderson, P. J. Index to American species of Phyllosticta. Mycologia **11**: 66–79. 1919.

margin may soon become irregular, and often several spots coalesce forming a large, indefinite, discolored area. As the lesions become older the diseased tissue becomes so papery and brittle that it breaks away from the healthy tissue, giving the leaf a ragged appearance as though it had been eaten by insects. This peculiar brittleness of the affected tissue, causing it to crumble to powder when rubbed between the fingers, is one of the constant symptoms of the disease. In the case of the smaller lesions in the

FIG. 2. SNAPDRAGON STEMS AFFECTED WITH PHYLLOSTICTA BLIGHT

A, Young stems with large brown lesions showing abundant pycnidia. *B*, Old stems showing white spots at base.

lamina, the center sometimes falls away, producing a shot-hole effect. Severely affected leaves may become completely withered, turn dark brown, and cling to the stems for a long time, resembling the leaves of the blighted branches. Several cases of the spreading of the infection from badly diseased leaves through the petiole and into the stem have been observed but this does not appear to be of constant occurrence.

On the stems. Both old and young stems may be attacked, the lesions occurring at any point and often appearing some time before any leaves are affected. Stewart,[5] however, says that it is "chiefly the succulent shoots" which are attacked. Observations of the writer have confirmed this statement for the branch blight form of the disease, that to which Stewart had reference. A water-soaked area suddenly appears on the young shoots several inches back from the tip and spreads rapidly around

FIG. 3. HEALTHY AND DISEASED SNAPDRAGON PLANTS

A, Healthy plant. *B*, diseased plant of the same age showing branch blight form of the disease and general dwarfing.

and lengthwise of the stem. In a few days the affected tissue shows a rather firm dark brown rot, then soon collapses and dries. Sometimes the whole shoot is affected, and becomes very brittle, the leaves also turning brown and shrivelling. At other times the spread of the water-soaked area is checked for some reason, leaving the terminal portion of the shoot green. In this case the collapsing and drying of the rotted area soon cuts off the water supply to the green tip, so that it gradually wilts, often fall-

[5] New York (Geneva) Agr. Exp. Sta. Bul. 179: 169.

ing over at the affected point. These were the symptoms which led Stewart to call the disease "branch blight" and "stem rot" (fig. 3b).

In addition to this blight or rot of the branches a form of the disease occurs in which more definite lesions are produced on the stems. These lesions are first visible as dark green, water-soaked and slightly sunken spots. In some cases, chiefly on old, woody stems the spread of the lesions soon ceases, a single spot being only two or three centimeters in length by one or two centimeters broad and oval in outline. Often several spots coalesce forming a large irregular patch which may nearly girdle the stem. Within a few days the center of the spots becomes ashy white and often split or cracked, the margin being dark brown or purplish, and small raised dots appear in large numbers scattered over the surface (fig. 2b). These dots, which at first are brown and later become black, are the pycnidia of the fungus. Lesions of this type appear most often at the base of the stem and can be distinguished from the lesions of the anthracnose only by the presence of these pycnidia and the fact that the blanched center of the spot lacks the blistered appearance found in the latter disease.

In other cases, usually in succulent stems, the spots enlarge very rapidly, sometimes spreading longitudinally for a distance of several inches, and often spreading horizontally so rapidly that the stem is completely girdled within a few days. These lesions do not become white or cracked or sunken but are yellowish to dark brown, with or without a heavy dark margin, and smooth, with numerous pycnidia arranged over the surface in close concentric circles (fig. 2a). The dead host epidermis adheres closely to the stem in these brown lesions, but in the white spots on woody stems it is very loose and brittle and flakes off easily.

On the plant as a whole the effect of the blight is a general dwarfing (fig. 3b). If any blossom spikes are produced they are so weak that they are unmarketable. No lesions, however, have been observed on the flowers themselves.

ETIOLOGY

The blight of snapdragons is caused by the pathogene *Phyllosticta antirrhini* Sydow. This fungus was originally described by P. Sydow[6] as occurring on leaves of *Antirrhinum majus* and was published by him as an hitherto undescribed species in Hedwigia in 1899. In 1900 F. C. Stewart[7] ascribed the stem disease which was first observed by him on snapdragons in a greenhouse at Geneva, New York, in 1898, to the presence of an undetermined species of Phoma.

[6] Hedwigia **38**: 134.

[7] New York (Geneva) Agr. Exp. Sta. Bul. 179: 109–110.

A comparative study of type material from Sydow's collection[8] and Stewart's original specimens,[9] together with material collected at Ithaca, New York, has shown that the morphology of the three organisms is identical. Specimens from Ithaca, sent to Stewart for examination, were pronounced by him to be affected with a fungus "without doubt" identical with that noted by him in 1900. Furthermore, as will be shown later, the fungus collected by the writer proved capable of producing all three types of symptoms (leaf spot, branch blight, and stem spot) and cultures obtained from leaves produced lesions on stems and those from stems produced lesions on leaves. From these facts it may be concluded that the fungus observed by Sydow, Stewart and the writer is the same and that it produces a disease of both stems and leaves of *Antirrhinum majus*

Attempts to discover a perfect stage of this fungus have failed so far. Old stems and leaves containing pycnidia were exposed out of doors through the winter, but repeated examinations of large amounts of material the following spring showed only pycnidia, some empty and some containing mature spores, to be present. Although the pathogene attacks both stems and leaves of the host, it seems best to retain for it the genus name Phyllosticta given by Sydow, since his was the first published description of the species.

Pathogenicity. By inoculation experiments with mycelium from pure cultures of the fungus, Stewart[10] practically demonstrated the pathogenicity of this organism. He inoculated snapdragon plants by puncturing the succulent shoots about three inches below the tip, inserting a bit of mycelium and covering the whole with grafting wax. In all cases the characteristic symptoms appeared, some of the branches being completely wilted within five days.

With pure cultures of the fungus, obtained by the methods described under "cultural studies" from diseased plants collected at Batavia and Ithaca, the writer has carried out additional inoculation experiments. Infections were obtained on both stems and leaves, and the fungus was reisolated from the lesions produced. Both mycelium and spore suspensions were prepared by crushing several mature pycnidia from pure cultures in a few cubic centimeters of sterilized water. In later experiments, spores from pycnidia taken directly from infected stems were used, the results being the same as those produced by spores from the pycnidia grown in pure culture.

[8] The writer is indebted to Dr. W. G. Farlow of Harvard University and Dr. F. J. Seaver of the New York Botanical Garden for their kindness in furnishing this material.

[9] Thanks are due F. C. Stewart, Botanist of the Geneva Agricultural Experiment Station, for his generosity in loaning his original specimens.

[10] New York (Geneva) Agr. Exp. Sta. Bul. 179: 110.

For the first experiment eight vigorous greenhouse plants of different varieties, growing in 8-inch pots, were selected. Three of the plants were wounded with a sterile scalpel at different points on the main stem and on the larger and smaller branches. Before wounding, the areas had been washed with a 1-1000 solution of corrosive sublimate and then with sterilized water. A small block of agar bearing mycelium was cut from the advancing margin of a culture and smeared over the injury. The part was then covered with moist cotton and wrapped with tinfoil. Three other plants were smeared with mycelium and covered in the same manner, except that no injury was made. One of the two remaining plants was used as a check for each set, being treated in exactly the same manner as the inoculated plants except that no inoculum was used. All the plants were kept in the greenhouse where the temperature ranged from 19° to 21°C. during the day and 7° to 10°C. at night. They were examined daily, and the cotton and tinfoil were removed on the third day. In the injured plants 100 per cent infection was obtained on the green stems and about 50 per cent on the red stems, the typical water-soaked lesions appearing on the second day. The lesions spread rapidly, taking on the characteristic colors, and some of the branches were completely wilted on the ninth day. Fruiting bodies appeared in the lesions on the third or fourth day. In the uninjured stems the percentage of infection was much less, and the lesions were several days later in appearing. In the check plants no lesions appeared at any time.

In the second experiment four plants were sprayed with a spore suspension by means of an atomizer, two then being covered with bell-jars for three days and two being left uncovered. Two check-plants were sprayed with sterilized water, one being covered with a bell-jar and the other left uncovered. All the plants were kept at the same temperature as those in the first experiment. No infections were obtained in those plants left exposed to the air, but in those covered with bell-jars lesions appeared on the leaves in seven days. Pycnidia appeared almost as soon as the lesions became visible. No infections were produced on any of the stems. Both checks remained perfectly healthy.

Later experiments were tried on a large number of plants and the following results were obtained:

Leaves inoculated by a smear of mycelium and covered with moist cotton occasionally showed infections, but in the cases observed, no pycnidia were developed in the lesions. The infections on the leaves rarely spread through the blade and petiole into the stem.

Stems of all ages became infected when mycelium was used as inoculum but lesions were most frequently obtained on young shoots. On old woody stems lesions were rarely produced and were small.

Although repeated trials were made, no infections of leaves or stems either by mycelium or by spores were obtained on plants kept in a cool house where the temperature did not run above 10°C.

Spore suspensions, whether of spores from pycnidia in culture or from those in host tissue failed in every case to produce lesions on the stems. An explanation of this and the preceding point will be given later.

Cultures obtained from stem lesions produced infections in both stems and leaves and those from leaf lesions produced infections on both leaves and stems.

The above experiments prove the ability of both the mycelium and the spores of the fungus to produce the disease. Reisolations were made from the various plants becoming diseased after inoculation, and in each case the fungus obtained was identical in all respects with that in the original cultures.

Life history. *Phyllosticta antirrhini* may pass the winter as pycnidia in old lesions on the dead stems and leaves. Many shoots of the snapdragon remain green all winter, especially in places where there is some protection, such as in rubbish piles, and are only partially decayed in the spring. Partially saprophytic mycelium is abundant within such shoots, especially the succulent ones, and in the very early spring begins to form pycnidia. These pycnidia are a much more prolific source of inoculum than the overwintered ones and have been found to contain mature spores as early as the middle of April. During periods of rainfall in warm weather, the spores are discharged from the pycnidia in gelatinous coils as described below and are carried to the young plants. This form of discharge makes it probable that wind, rain and possibly insects may be the carriers of the conidia. The fact that infections occur so commonly at the tips of leaves where, due to the conformation of the snapdragon leaf, drops of water always collect after a rain, would seem to indicate that rain drops are the common carriers of spores, at least to the leaves.

In the greenhouse the pathogene may be carried over from season to season in several ways: as mycelium or pycnidia on plants brought in from the garden, in debris left in the benches, in plants moved from house to house. The spores may be disseminated by several agents, such as air currents, insects, or the hands of those who work with the plants, but probably the most important are the drops spattered about in watering the plants.

Under the proper conditions of moisture and temperature the spores germinate readily on the surface of the host and produce infections.

A detailed study of infection has been made for the leaf only, but the main features of the process are doubtless similar in the stem since the

epidermal structure in the two organs is practically the same. Vaughan's[11] method of preparing material in toto proved the most useful for this work, though even with careful manipulation it did not invariably give good results. Small drops of water containing spores were placed on leaves laid on damp filter paper in moist chambers, in some cases the drops being on the upper, and in others on the lower, surface of the leaf. After being kept in a warm room for about forty-eight hours, the moist chambers were opened and the drops allowed to dry down on the leaves. The inoculated areas were then cut from the leaves and killed and fixed in Duggar's fixer (equal parts glacial acetic acid and 95 per cent alcohol). Since the cuticle of the snapdragon leaf is very thick, it was found necessary to puncture the tissue with a needle in order to secure rapid penetration of the fixer, and to soak the material in 95 per cent alcohol overnight before washing

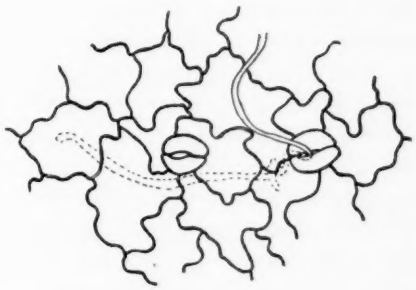

FIG. 4. TIP OF LONG GERMTUBE OF PHYLLOSTICTA ANTIRRHINI ENTERING LEAF THROUGH STOMATE AND PENETRATING EPIDERMAL CELLS
Camera lucida. × 600

to completely decolorize it. From the 95 per cent alcohol the bits of leaf were carried back to 50 per cent alcohol, washed in several changes of the latter and then stained with Pianeze III B for fifteen to thirty minutes. When the proper reactions are obtained the pink spores and germ-tubes stand out in sharp contrast to the pale green cell walls of the host.

The method of penetration is the same whether the germinating spore lies on the upper or on the lower surface of the leaf. The slender germ-tube grows over the surface for a considerable distance, finally turning downward at the tip and entering a stomate. The first stomate encountered is not always the one entered. The germ-tube is usually non-septate and unbranched when it enters the leaf, but several cases were observed in

[11] Vaughan, R. E. A method for the differential staining of fungous and host cells. Missouri Botanical Garden Annals **1**: 241–242. 1914.

which branching had occurred and the tips of the branches had entered different stomates.

The presence of hydathodes at the tips of the leaves, offering even larger openings than the stomates for the entrance of the germ-tubes, may partly explain the frequent occurrence of lesions at the tips.

From the substomatal cavity the germ-tube enters the epidermal cells and infection is established (fig. 4).

Morphology. In the host tissue the mycelium is both inter- and intracellular, but no haustoria have been found. The mycelium is hyaline, irregular and stout, varying from 3 to 6μ in diameter. It is divided into many small cells by numerous septa and is profusely branched.

Sometimes simultaneously with the development of the lesions on the stems, sometimes several days later, the pycnidia become visible. On the leaves their appearance is usually delayed from one to several weeks after that of the lesion. They are imbedded in the tissue of the host, but are easily visible to the naked eye as small black papillae.

The development of these pycnidia presents no unusual features. The hyphae in the host tissues form a close gnarl just under the cuticle in the stem or just beneath the upper epidermis of the leaf, this gnarl forming the pycnidial wall made up of an outer layer of thick-walled pseudoparenchymatous tissue and an inner thin-walled layer. The mature pycnidium (fig. 5) is of the typical flask shape and protrudes slightly above the ruptured epidermis or cuticle of the host. The very short neck is made up of exceedingly heavy-walled cells, which give it the appearance, in surface view, of a black ring in contrast to the brown walls of the body. In size the mature pycnidia vary from about 56μ to 260μ in diameter, the average being about 100μ. Sydow describes them as measuring 100μ to 180μ in diameter.

The cavity of the pycnidium is lined with a layer of thin-walled hyphae which stain very slightly. From this layer the minute (1 by 3μ) cylindrical conidiophores arise (fig. 5). The small hyaline pycnospores are cut off from the conidiophores by constriction. They are produced in great numbers and are imbedded in a gelatinous matrix, the whole mass completely filling the cavity of the pycnidium. In the presence of moisture the gelatinous matter swells and the spores are extruded from the ostiolum, held together in a long whitish coil. Some idea of the large number of spores formed in a single pycnidium may be gained from the fact that the complete emptying of a pycnidium of average size was observed to require twenty-three minutes, the coil of spores attaining a length of over 8 cm.

The pycnospores (fig. 6) are cylindrical with blunt rounded ends to nearly ellipsoid. They are biguttulate, hyaline, 4 to 6 by 1 to 2μ (usually 4 by 2μ), (4 to 6 by 1.5 to 2μ, Sydow).

When placed in tap water, distilled water, or snapdragon leaf decoction or on potato agar, and kept in a warm place, the spores from mature pycnidia germinate within eighteen to twenty-four hours. Spores placed in drops of water and on very thin films of potato agar on the inverted covers of van Tieghem cells, and kept from 23° to 29°C., gave nearly 100 per cent germination in about eighteen hours, growth of the hyphae being much more profuse in the agar film.

At temperatures lower than 18°C. or higher than 47°C. or in the absence of a film of water germination does not occur. Spores placed on dry covers

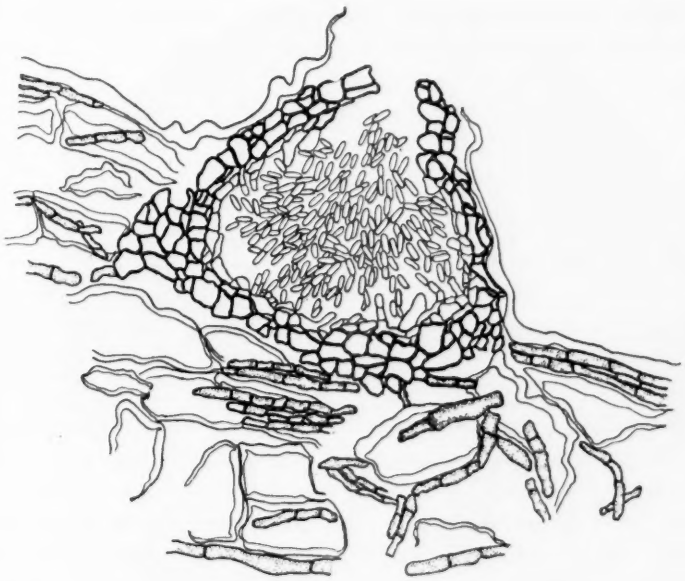

FIG. 5. MATURE PYCNIDIUM OF PHYLLOSTICTA ANTIRRHINI IN CORTEX OF HOST STEM

Longisection. Most of spores have been extruded. Camera Lucida. × 600.

of van Tieghem cells, or in drops of water so small that they soon dried off, failed to germinate, although the air of the cell presumably was kept moist by the large drop of water in the bottom. Spores kept at a temperature of 47°C. or higher and 18°C. or below did not germinate at all, while those kept at 20° to 21°C. gave a small percentage of germination, the germ-tubes, however, not developing into mycelium.

The first evidence of germination of the spore is a marked swelling, followed by the appearance at the end of the spore of a stout germtube, almost as large in diameter as the spore itself. One or two germtubes are

sent out from one end of the spore, or a tube emerges from each end (fig. 6). The germ-tubes elongate rapidly and become septate, soon branching to form the mycelium.

A consideration of the factors governing germination in the above tests may explain the negative results obtained in certain of the inoculation experiments. No infection was produced when plants inoculated with a spore suspension were kept in a house where the temperature did not rise above 10°C. Since a temperature of 20°C. or higher is most favorable for spore germination, infection probably failed because no germination occurred. The host stems of *Antirrhinum majus* are provided with a heavy cuticle and so shed water and dry off rapidly. Thus it is possible that in the case of the stems sprayed with a spore suspension, although the plants

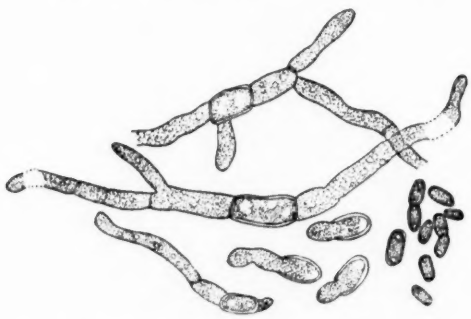

FIG. 6. MATURE AND GERMINATING PYCNOSPORES OF PHYLLOSTICTA ANTIRRHINI
Note swelling at germination. Camera lucida. × 625

were kept in a warm house, infection failed because the drops of water containing spores did not adhere long enough for germination to take place. If any of the spores adhered, the necessary film of water may have been lacking, preventing germination in this way.

CULTURAL STUDIES

Pure cultures of *Phyllosticta antirrhini* were repeatedly obtained in the following manner:

Pieces of diseased stems or leaves were disinfected on the surface by immersing in 95 per cent alcohol for several seconds, then soaking in 1–1000 corrosive sublimate solution about one minute. They were rinsed in five changes of sterilized water and bits of the infected tissue were then taken out with sterilized forceps and transferred to sterilized media.

In obtaining pure lines of the fungus, single hyphal tips were cut from the margin of vigorously growing young cultures by means of a sterile

sharp-pointed scalpel and transferred to new media. This method was found to be more satisfactory than the single spore method, on account of the difficulty of locating the small hyaline spores in a poured plate.

Observations on the cultural characters of the fungus were made with only the more common solid media: potato, oatmeal, bean, cornmeal, and nutrient agars, bean plugs; and with beef bouillon. Some marked differences in the growth on the various solid media were noted.

On nutrient agar the growth of *Phyllosticta antirrhini* is very slow and weak, and fruiting bodies are not produced.

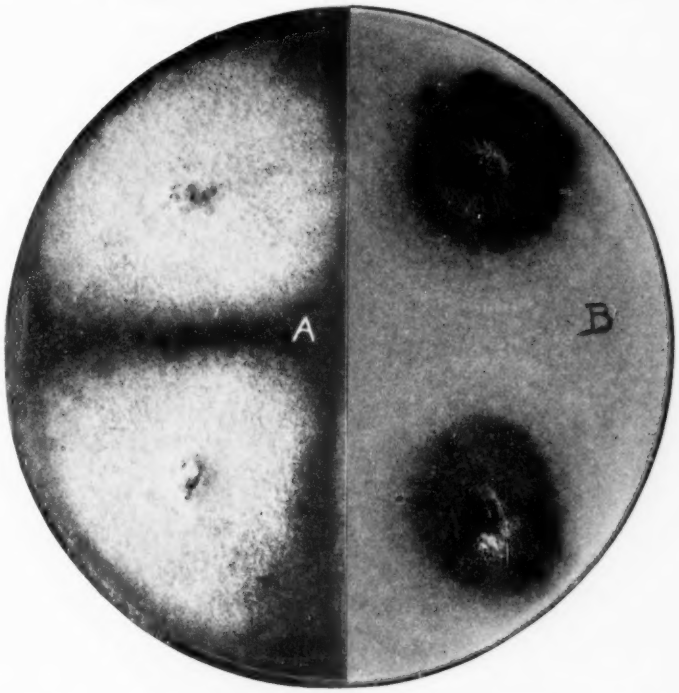

FIG. 7. GROWTH OF PHYLLOSTICTA ANTIRRHINI ON POTATO AND CORNMEAL AGAR, FIVE DAYS

A, Yellowish white growth on potato agar. *B*, Greenish black growth on cornmeal agar.

The growth of the hyphae in beef bouillon is very rapid. The medium is permeated by mycelium in several days, and a heavy yellowish grey pellicle is formed at the surface. No fruiting bodies are formed in this medium.

In potato and bean agar the growth of the fungus is rapid and profuse, becoming visible macroscopically within twenty-four hours after planting.

The typical growths on these media are low (aerial hyphal branches not more than 0.5 mm. high) and thin, the hyphae penetrating the substratum only slightly. In color the growths are yellowish and smooth below, sordid white and floccose above, with a nearly colorless zone at the extreme margin. The pycnidia appear early, usually within two or three days after the mycelium becomes visible. They are at first brownish, then become black, and are scattered in concentric circles around the oldest part of the planting, soon becoming abundant and dotting the whole surface. Older cultures (about eight days) are distinctly zonate. In cultures several months old, the early growth is overgrown by a thick, black, stroma-like crust which is glossy, except where a scanty white mycelium still persists. Pycnidia formed in this crust are larger but less abundant than those produced in the young, vigorously growing cultures.

On oatmeal and cornmeal agar the growth is similar in form to that on the potato or bean agar, but is strikingly different in color. As early as the third day after planting the growth is greenish black, with a more or less glossy surface and with a colorless band at the extreme margin. The color is located in the mycelium itself, and is not due to a discoloration of the medium. Pycnidia are produced as abundantly as in potato and bean agar, and the same zonate character appears in cultures five to seven days old. Old cultures (three to four weeks) are uniformly dull-black, the zonate character having disappeared.

The typical young cultures on the two types of agar are shown in comparison in figure 7.

PATHOLOGICAL HISTOLOGY

In both stems and leaves the lesions produced by this disease are necrotic. The mycelium is inter- and intracellular as already stated. In the stems it is found beneath the cuticle and between the cells in long strands made up of several parallel hyphae, while within the cells single hyphae pass from lumen to lumen. Apparently the mycelium is able to penetrate the walls of the softer cells directly but must enter the thicker walled cells such as the tracheids through the pits. All types of tissue with the possible exception of sclerenchyma are attacked. Vessels are rarely invaded. The epidermal cells are the first to be invaded, the mycelium spreading from them to the outer cortical cells, then progressing more deeply into the stem through the phloem and cambium regions to the xylem and pith. Injury to parenchymatous cells is apparent several cells in advance of the mycelium. The contents of such cells are completely destroyed. They are first broken down, then disappear entirely. The empty walls soon collapse leaving the tissue merely a mass of broken

walls and tangled hyphae. The presence of the hyphae produces no apparent effect on the invaded lignified cells (fig. 8).

The histological changes which occur in the leaf are similar to those seen in the stem. The same destruction of the soft tissues takes place, while the veins are penetrated but remain intact. The mycelium formed from the germ-tube attacks first the epidermal cells, spreading in all directions from the point of penetration. The epidermal cells are killed rapidly, and the palisade cells are next attacked. These cells soon die and the infection spreads downward through the leaf until finally all tissues are involved.

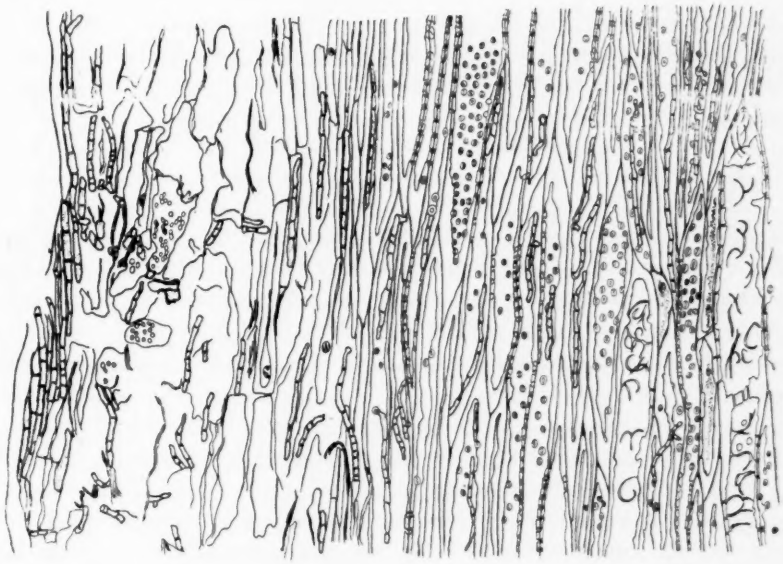

FIG. 8. PATHOLOGICAL EFFECT OF PHYLLOSTICTA ANTIRRHINI ON TISSUES OF YOUNG SNAPDRAGON STEM

Note disintegration of cortex, phloem and cambium regions and invasion of xylem elements. The mycelium is seen passing through the pits of the xylem cells. Camera lucida. × 202.

The successive stages in the disintegration of the cells of both leaves and stems are easily studied in microtome sections cut about 5μ thick. Satisfactory results are obtained in staining such material with either Flemming's triple stain or Heidenhain's iron alum-haematoxylin.

The cytoplasm is the first to show the effects of the presence of the fungus. Before the cell wall is penetrated by the hyphae, the cytoplasm, probably attacked by some toxin or enzym secreted by the advancing mycelium, breaks up into coarse granular particles and finally disappears alto-

gether. The nucleus remains visible for a time but soon breaks up and disappears in its turn. The chlorophyll bodies, when present, are the last to disappear, and may often be found apparently intact for some time after the walls are empty of other content. At length they too disappear. The cell walls may collapse soon after the breaking up of the cytoplasm, or they may remain normal for a time after all contents are destroyed, even though penetrated by hyphae. Eventually, however, they collapse and become more or less broken.

The line of demarcation between the healthy and diseased tissues is very sharp, but no evidence of cork formation or of suberization could be discovered.

The collapse of all soft tissues in both stems and leaves is responsible for the sunken appearance of the lesions, and the complete breaking down of the cells and drying of the tissues causes the brittleness and ready crumbling of the affected areas described under symptoms.

CONTROL

Little work has as yet been done on the control of the Phyllosticta blight. Stewart[12] offers the suggestion that spraying with Bordeaux mixture as for anthracnose may be efficacious. It seems probable also that dusting with sulfur would control this blight. This method would give the additional advantage of controlling the rust at the same time. The planting of snapdragons in gardens where the disease was prevalent the preceding year should be avoided unless all debris can be removed.

From the observations of the conditions required for spore germination and from the results obtained in the inoculation experiments, it seems possible that in greenhouse plants the disease can be greatly diminished if not entirely controlled by certain precautionary measures. The first is of course the removal of all debris from infested benches before new plants are put in and the use of only healthy plants for setting. The second precaution is the practice of soil watering, with proper ventilation of the house. Finally, snapdragons should be grown in cool houses, for the plants will do well in an average temperature of 15°C., a temperature at which the fungus can not thrive as a parasite.

[12] New York (Geneva) Agr. Exp. Sta. Bul. 179: 110.

PHOMOPSIS JUNIPEROVORA, A NEW SPECIES CAUSING BLIGHT OF NURSERY CEDARS

GLENN GARDNER HAHN

WITH ONE FIGURE IN THE TEXT

In the writer's early studies of the nursery blight of cedars (3) an undetermined organism was isolated from *Juniperus virginiana* L. and found to be the causal fungus. At that time this fungus was referred temporarily to the genus Phoma, until determination work of a more complete nature had been accomplished.

By growing the fungus secured from a series of isolated spores, in pure culture upon corn meal agar and prune agar in petri dishes, and steamed rice and corn meal in flasks, fruiting bodies were secured, but these in no case observed were of an ascigerous stage. Sections of the pycnidia produced by the inoculation of *J. virginiana* in the greenhouse showed abundant occurrence of scolecospores (The A and β type spores of Diedicke (1)) characteristic of the genus Phomopsis (2). Field material which previously had shown apparently only A type spores and what appeared to be a Phlyctaena, upon further sectioning and examination showed β type spores occurring in the same pycnidium with the A spores. This observation of the two spore types, together with the observation as to the nature of the pycnidium (which, as was earlier indicated, did not refer the fungus to a typical Phoma), definitely shows the organism to belong to the genus Phomopsis, and inasmuch as it differs from all other fungi so far described as infectious to *J. virginiana* and from all other Phomopses upon conifers, it is now described as *Phomopsis juniperovora* n.sp., having the following characteristics:

Phomopsis juniperovora n.sp. (fig. 1, A)

Pycnidiis sparsis, fuscis, carbonaceis, lenticularibus, conoideis, vel truncatis bis subglobosis; initio subepidermicis denique erumpentibus, astromatoideis, ostiolatis vel non definite ostiolatis, contextu heterogeneo praeditis, matricibus saepe supra cavitates sporiferas incrassatulis; in foliis,—epiginis, raro hypogenis, lenticularibus bis subglobosis, unilocularibus, 124–310μ diameter, vulgo 200μ; in truncis—conoideis, truncatis vel lenticularibus, basi latis, depressis, unilocularibus, matricibus proliferis frequenter disseptimenta formantibus; 186–620μ diameter vulgo 350μ.

Sporulis ellipsoideis, oblongis vel fusiformibus hyalinis, continuis, biguttulatis, 6.5 to 12 by 1.8 to 3.5μ, vulgo 7.5 to 10 by 2.5 to 3μ. Basidiis filiformibus, attenuatis, con-

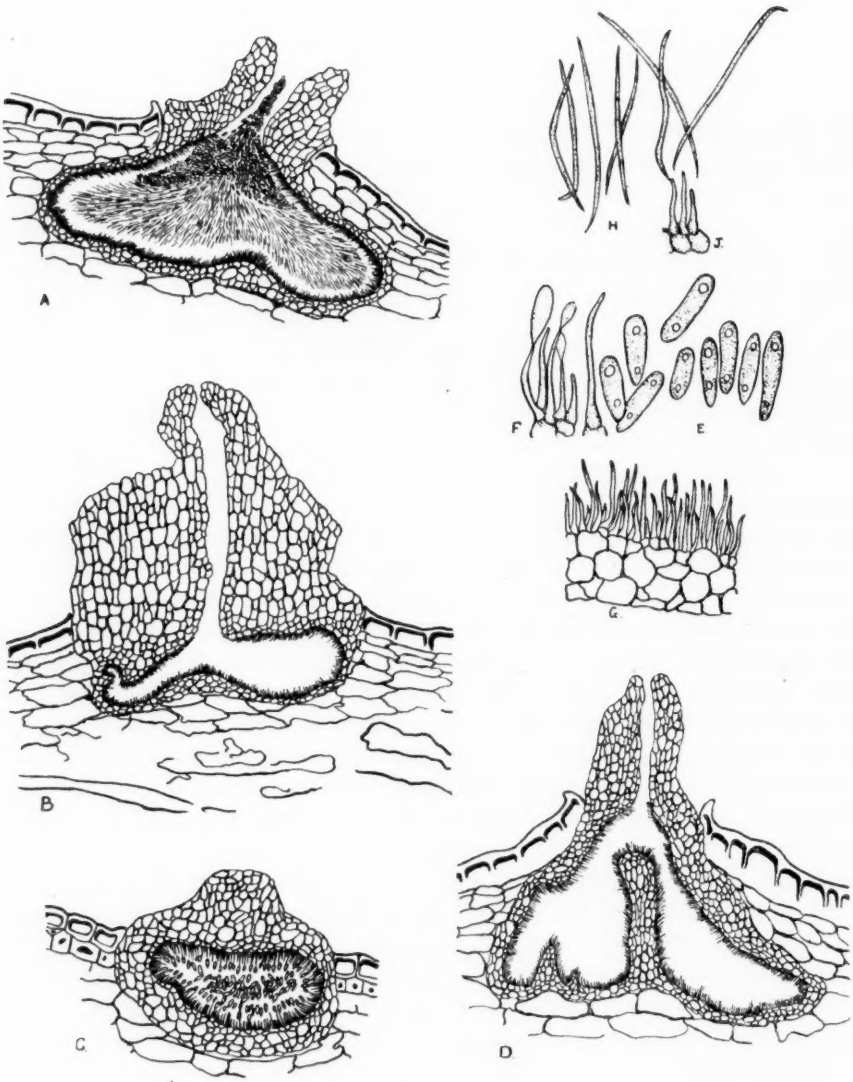

FIG. 1

A. A typical pycnidium of *Phomopsis juniperovora* upon the stem, showing both A and B type spores. Drawn with the aid of the camera lucida. Approximately 113 ×.

B. Pycnidium upon the stem, showing the dense pseudoparenchymous layer overlying the spore cavity. It is this growth which breaks through the epidermis, frequently before spores are formed. The chimney-like ostiole is characteristic. Drawn with the aid of the camera lucida. Approximately 113 ×.

tinuis, subulatis, 5 to 15 by 1 to 2μ. Scolecosporulis filiformibus, rectis, vel leviter curvulis, vel hamatis, raro sigmoideis, 17.5 to 28 by 1μ, vulgo 20 to 24 by 1μ. Basidiis brevibus, subulatis, 5μ.

Hab.—In acibus et truncis Juniperi virginianae, Dundee, Ill. 1916.

Pycnidia lens-shaped, conical, truncate, at times subglobose typically depressed with a broad base; embedded at first but becoming erumpent by the upper part of the pycnidium breaking through the epidermis before or with maturity; separate; without a stroma; texture, heterogeneous; the spore-bearing cavity floored below by a layer of faintly colored cells, two to several thick, and roofed above with a denser layer, at times exceedingly thick; (fig. 1, *B*); toward the outside the cells may be considerably darker, brown or black, ostiolate but generally provided with an opening slit or irregular orifice; upon the leaves, lens shaped to subglobose (fig. 1, *C*), epigenus, always simple chambered, 124 to 310μ diameter, average 200μ; upon the stem, cone shaped, truncate or lens shaped, simple chambered, frequently with rudimentary partitions arising from the proliferous layer, usually from the lower floor or base of the cavity (fig. 1, *D*), 186 to 620μ diameter, average 350μ. Spores oblong to ellipsoid, or spindle shape, with subacute extremities, usually biguttulate, occasionally with more than two oil drops, hyaline, continuous, 6.5μ to 12 μ by 1.8 to 3.5μ (100 measurements) (fig. 1, *E*) commonly 7.5 to 10μ by 2.5 to 3μ; sporophores filiform, linear, subulate, often slightly curved, 5 to 15 by 1 to 2μ (fig. 1, *F*) in close set, compact layers, persistent (fig. 1, *G*).

Associated with the A spores and produced in the same pycnidium are β spores or scolecospores. These may also occur alone in fruiting bodies approximating the Phlyctaena genus type. The second spore forms are long, filamentous, occasionally curved S-shaped, or hooked at the upper end, 17.5 to 28μ by 1μ, generally 20 to 24μ by 1μ (fig. 1, *H*). Sporophores short subulate, about 5μ (fig. 1, *J*).

Spores extruded in a cream colored, gelatinous tendril 1 to 5 mm. long, becoming brittle upon drying.

Type specimen in the Pathological Collections, B. P. I., U. S. Department of Agriculture, and Office of Investigations in Forest Pathology (F.

C. Pycnidium upon a leaf. Drawn with the aid of the camera lucida. Approximately 197 ×.

D. Pycnidium upon the stem showing false partitions arising from the floor of the spore-bearing cavity. Drawn with the aid of the camera lucida. Approximately 113 ×.

E. Typical A type spores. 1125 ×.

F. Sporophores of A type spores. 1125 ×.

G. Proliferous layer and sporophores. 563 ×.

H. B type, or scolecospores. 1125 ×.

J. Sporophores of B type spores. 1125 ×.

P. Nos. 25002, 25005) on diseased *Juniperus virginiana* L., nursery grown stock, three years old, from Dundee, Ill., June 1916.

Distribution. Nebraska (3); nursery stock of *J. virginiana* L. in Kansas, Illinois, Minnesota, Iowa,[1] Ohio, New York, Pennsylvania.

CULTURAL CHARACTERISTICS

The cedar blight organism grows well on corn meal agar, prune agar, steamed rice, and steamed corn meal. It fruits more frequently on the corn meal agar and on the corn meal flasks, than on the other media mentioned.

Growth of the fungus is silky, appressed on corn meal agar in petri dishes, with or without a slight tendency to zonate, at first empire yellow (4), becoming orange rufous after twenty days. The pigment is diffused throughout the medium, in a radius of 10 mm. beyond the extending edge of the colony. This is accompanied by the formation of flaming orange crystals, which may occur within twelve days. These crystals are observed less abundantly on prune agar. Here color pigmentation passes through the same shades during the early development of the colony, but finally becomes tawny. Growth characteristics very much resemble those upon corn meal agar.

COMPARISON WITH OTHER SPECIES OF PHOMOPSIS ON CONIFERS

In the literature exceedingly few species of Phomopsis have been described on conifers, although undoubtedly others will be found which at the present time are described under other genera. A Phomopsis occurs on *Thuja occidentalis* L. in Europe and has been described by Diedicke as *P. thujae* Died. n. sp.[2] This fungus very much resembles the *P. juniperovora* in that it apparently has the same morphological features as to the nature of its pycnidium. The A spores, however, differ in that the foreign species has a smaller spore, 5 to 8 by 2μ. The *P. juniperovora* spores are longer and wider. Unfortunately specimens of the *P. thujae* in the Pathological collections, U. S. Department of Agriculure, distributed as No. 1018 Exsiccatus Sydow Mycotheca germanicus[3] proved to be only a species of Diplodia, so exact comparison was impossible. A note accompanying the foreign specimens states that the *P. thujae* is frequently as-

[1] Specimens sent from a nursery at Kent, Iowa, (1896), to Dr. F. C. Stewart, N. Y. (State) Exp. Station (Phytopathology, **8**: no. 1. Jan., 1918). Later, collections of material were also received by the Office of Forest Pathology, B. P. I., U. S. Dept. Agr., from this State (1916).

[2] Kryptogamenflora der Mark. Brandenberg, **9**: 275. 1912–1915.

[3] Annales Mycologici. **9**: 557. 1911.

sociated with a mature Diplodia. Evidently only Diplodia material was sent over.

It is here interesting to note that the parasitism of *P. juniperovora* has been proven positively upon young nursery trees, in the greenhouse, of *Thuja occidentalis* and *T. orientalis* L. At the same time inoculations upon three pines, *Pinus edulis* Engelmn., *P. glabra* Walt., and *P. taeda* Linn., gave negative results, as well as upon *Pseudotsuga taxifolia* (Lam.) Britton, *Picea parryana* (André) Parry, *P. engelmanni* Engelmn., and *Abies lasiocarpa* (Hook) Nutt.

That the *Phomopsis juniperovora*, now a widely known distributed parasite upon young nursery cedars, particularly red cedar, is distinct from the European fungus of Diedicke is the opinion held; however, it is interesting here to call attention to a possible similarity between the two. The identity of the *Phomopsis thujae* Died. with the native Phomopsis on nursery cedars cannot be definitely established until a direct morphological comparison has been made from type material, and cross inoculation has been performed to prove parasitism.

OFFICE OF INVESTIGATIONS IN FOREST PATHOLOGY
U. S. BUREAU OF PLANT INDUSTRY
WASHINGTON, D. C.

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PHYTOPATHOLOGICAL NOTES

Annual general meeting of the Association of Economic Biologists. Mr. W. B. Brierley, Botanical Secretary, has furnished a brief report of the annual meeting of the Association of Economic Biologists, which was held in the Imperial College of Science on December 10 and 11, 1919. Over seventy new members joined the association. Sir David Prain, C.I.E., C.M.G., F.R.S., was elected president for the ensuing year.

Wednesday morning was devoted to short communications and exhibitions, upon each of which there was an active discussion. Mr. E. E. Green was in the chair. Mr. A. D. Cotton showed a collection of very beautiful photographs of tree diseases prevalent in the United States. Mr. W. F. Bewley showed tomato diseases destructive in the Lea Valley glass houses. A Tingid bug, attacking Rhododendrons, was exhibited by Mr. E. E. Green; whilst Mr. W. B. Brierley described a growth of *Citromyces pfefferianus* in pure deci-normal sulphuric acid, which had been sent to Rothamsted by Dr. Golding of Reading.

On Wednesday afternoon the following papers were read and discussed, Mr. A. G. L. Rogers occupying the chair: Mr. W. F. Bewley on "Sleepy Disease or Wilt of Tomato." The pathogen has been named *Fusarium lycopersici*, but this is composed of two discrete fungi, a parasitic *Verticillium* sp., and a saprophytic *Fusarium* sp., the former being the so-called *Diplocladium* stage. The pathogenicity of the *Verticillium* sp. is conditioned by a temperature factor, and there are various strains differing constantly in physiological properties.

Mr. W. E. Hiley on "A new Instrument for Measuring the Light Intensity in Woods." Solutions of chlorophyll and pure spirit are connected by a copper-constantin thermocouple and a current of about 1–3 by 10^{-5} amperes obtained, which on a sensitive galvanometer gives a deflection of two inches. The instrument will be used in measuring the light intensity necessary for the growth of shade-bearing trees used for underplanting light demanders, and to test the value of forest weeds as indicators.

Mr. F. R. Petherbridge on "The Life History of the Strawberry tortrix, *Acalla comariana*." The life history of the tortrix, its distribution, and the damage it causes, were described, and remedial treatment indicated.

Thursday was devoted to a symposium on "The integration of mycological research with practice in Agriculture, Horticulture, and Forestry." Dr. F. Keeble occupied the chair.

Sir Daniel Hall discussed the Administrative problem. The relation of "free" to "administrative" research was dealt with, the former being controlled by a University or kindred body and only remotely subject to government criticism; the latter being an integral part of the government's activities. The advantages and disadvantages of directed team work were discussed and administrative difficulties in this connection indicated. In dealing with plant diseases the Board of Agriculture proposes the following organization:—

(I) The institutions engaged in free research.

(II) The Board's own staff of advisors and inspectors dealing with administrative research.

(III) A corps of local investigators attached to the agricultural colleges.

It is anticipated that it will be possible through the Councils of Research and Advice to keep these bodies so far in touch that from time to time combined investigations can be undertaken of particular widespread and pressing problems.

Prof. V. H. Blackman discussed the training problem. Emphasis was laid on the fact that the prospects of a career must be sufficiently satisfactory to attract students of high ability. A wide outlook is essential in this work and students must not only have a good general knowledge of physics and chemistry, but a thorough grounding in botany and special training in mycology, mycological technique and plant pathology. No attempt should be made to produce a fungal systematist. Acquaintance with the results of plant breeding is advisable, as well as of medical bacteriology and entomology. The physiological outlook is essential and field experience very important.

Dr. E. G. Russell discussed the agricultural problem. Emphasis was laid on field study of the growing plant in health and in disease, both states being regarded as the resultant of the prevailing conditions. The extreme complexity of the problems was pointed out and illustrations given of the ways in which they are being attacked at Rothamsted. The relations between the central research station for fundamental investigations and the small research sub-station devoted to particular aspects of crop production was indicated. The special difficulties of mycological research on agricultural crops were dealt with, together with the best methods of approach to the general problems, and it was concluded that in essential principles the work was more in common with that done among human beings on public health and eugenics than with curative medicine.

Mr. F. J. Chittenden discussed the horticultural problem. The main problems confronting the mycologist in horticultural practice were indicated and the special difficulties described. These largely result from the intensive methods used, the vast variety of plants grown, many of

very limited adaptability, the controlled conditions of cultivation, and the transference of plants from place to place. The task of the mycologist is not only to devise such methods of control as are practicable under the conditions imposed, but to bring these home to the practical man. Emphasis was laid on the value of demonstration gardens as a means of education.

Prof. W. Somerville discussed the forestry problem. The peculiar difficulties of mycological research in relation to forestry arise in the fact that in practice the returns are long deferred, the annual value of the output per acre is relatively small, the operations are conducted in less accessible areas, and the crop (trees) is less amenable to treatment. The possibility of breeding immune varieties and the difficulties involved were indicated. Emphasis was laid on the necessity for pure research, but the diffusion of its results among practical foresters is not easy, owing to the obstacles involved in testing conclusions on a crop which may not mature for a century. The importance of the present widespread changes in land ownership and the bearing of the functions of the newly created Forestry Commission upon the new conditions introduced, was dealt with. It was concluded that it is in the improvement of education all round that we may most hopefully look for continued appreciation of science and that when this advance has been secured the integration of research with practice will be a natural and inevitable consequence.

Sir David Prain briefly described the functions of the Imperial Bureau of Mycology, now being formed, and its relation to existing institutions.

The general discussion in the afternoon was opened by Mr. E. S. Salmon, and the following took part: Messrs. Brooks, Cotton, Brierley, Henry, Bruce, Taylor, Lister, Gough, Bewley, Willis, Ramsbottom, Wormald, Paine, Keeble, and the Misses Cayley and Wakefield.

Check list of Department of Agriculture publications. There are still on hand available for distribution copies of the "Check List of publications of the Department of Agriculture on the subject of Plant Pathology, 1837–1918," which was issued in June, 1919, as Bibliographical Contributions No. 1 of the U. S. Department of Agriculture Library. Copies may be procured by application to the Library, U. S. Department of Agriculture, Washington, D. C.

Personals. Dr. L. O. Kunkel resigned the position of plant pathologist in the U. S. Department of Agriculture, on February first, to become associate pathologist of the Hawaiian Sugar Planters' Experiment Station, Honolulu. He will be engaged in work on the mosaic disease of sugar cane.

Dr. B. O. Dodge, for several years a member of the Department of Botany of Columbia University, has accepted a position as plant pathologist in the office of Fruit Disease Investigations, U. S. Department of Agriculture.

Mr. Charles R. Hursh has resigned his position as assistant pathologist in Cereal Disease Investigations to take up graduate study at the Missouri Botanical Gardens.

Dr. E. Mead Wilcox has resigned as professor of plant pathology in the University of Nebraska and plant pathologist of the Experiment Station, effective April 1, 1920, to accept the directorship of the Agricultural Experiment Station being established at Santo Domingo in the Dominican Republic.

Washington meeting of the Advisory Board of American Plant Pathologists. The Advisory Board met in Washington January 29 to 31 with the following commissioners present: C. R. Orton, L. R. Jones, E. M. Freeman, H. S. Jackson, A. H. R. Buller, and G. R. Lyman. The first session was held at the headquarters of the National Research Council on the invitation of Dr. C. E. McClung, Chairman of the Division of Biology and Agriculture. The Advisory Board is the committee on Phytopathology of the Research Council and this meeting not only afforded an opportunity for the Board to consider important matters referred to it by the Council, but also enabled the members of the Board to become personally acquainted with the officers and work of the Council.

Detailed consideration was given to the Phytopathological Institute in consultation with officers of the National Research Council. Dr. Freeman, Chairman of the committee on securing funds, spoke on the proposed Institute at a special meeting of the Pathological Seminar of the Bureau of Plant Industry. It is felt that definite progress is being made in developing a wide-spread interest in the Institute and that the prospects are good for its realization in the not distant future.

The status of the various coöperative projects of the Board was considered. There is imperative need for funds to permit the leaders of these projects to push this work and to properly correlate the results obtained. That American plant pathologists have the spirit of coöperation is clearly shown by the discussions at the St. Louis meeting, but the effective prosecution of coöperative projects requires funds to permit conferences of the coöperators, the securing of uniform material, and the comparison of results. It is hoped that such funds can be secured, either through the agency of the National Research Council, or independently. In accordance with the vote of The American Phytopathological Society at St. Louis the Advisory Board took steps to inaugurate coöperation on dusting as

a means of plant disease control. Dr. N. J. Giddings of the West Virginia Experiment Station was requested to assume leadership and those interested in this project should communicate with him.

One of the most important topics before the Advisory Board at this meeting was the consideration of plans for a summer field meeting during 1920. It was determined to hold such a meeting about the first week in August with particular reference to fruit diseases. The tentative itinerary decided upon involves assembling at some point in the Shenandoah Valley, probably at Winchester, Va., whence passage will be made by automobile northward through West Virginia and Maryland to the Gettysburg section of Pennsylvania. The duration of the conference will be three or four days. The itinerary contemplated covers one of the most attractive sections in the eastern United States,—agriculturally, historically and scenically. Careful consideration was given to plans for inviting pathologists from abroad to visit the United States at the time of this field meeting. This matter was finally left in the hands of a committee consisting of G. R. Lyman, C. L. Shear, and W. A. Orton. The following committee on arrangements was appointed to have charge of perfecting plans and making all arrangements for the Shenandoah Valley conference: F. D. Fromme, chairman, representing Virginia; N. J. Giddings, representing West Virginia; C. E. Temple, representing Maryland; C. R. Orton, representing Pennsylvania; M. B. Waite, representing The Bureau of Plant Industry; G. R. Lyman, representing the Advisory Board.

G. R. LYMAN,
Chairman.

LITERATURE ON PLANT DISEASES[1]

COMPILED BY ALICE C. ATWOOD, AND FLORENCE P. SMITH, BIBLIOGRAPHICAL ASSISTANTS, BUREAU OF PLANT INDUSTRY

January, 1920

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All authors are urged to cooperate in making the list complete by sending their separates and by making corrections and additions, and especially by calling attention to meritorious articles published outside of regular journals. Reprints or correspondence should be addressed to Miss E. R. Oberly, Librarian, Bureau of Plant Industry, U. S. Dept. of Agric., Washington, D. C.

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APPENDIX

REPORT OF THE ELEVENTH ANNUAL MEETING OF THE AMERICAN PHYTOPATHOLOGICAL SOCIETY

The eleventh annual meeting of the Society was held in Soldan High School, St. Louis, Missouri, December 29, 1919, to January 2, 1920, in conjunction with the American Association for the Advancement of Science and the Botanical Society of America. The Society headquarters were at Marquette Hotel.

About ninety members were present. One hundred and forty-four new members were elected, making the total active membership of the Society five hundred and twelve on January 1, 1920.

Forty-nine papers were presented at the regular sessions. Abstracts of these appeared in the January number of PHYTOPATHOLOGY. One session was devoted to consideration of the topic "Eradication of Plant Diseases: Is it Practicable, and when should it be Attempted?" Certain phases of this question were presented briefly by selected speakers, after which there was general discussion.

Three sessions were held jointly with other societies. The first of these was held Tuesday afternoon, December 30, with Section G of the American Association for the Advancement of Science and the Botanical Society of America. At this meeting the address of the vice president of Section G was presented, and also invitation papers on phylogeny of seed plants. The second session was held Thursday afternoon, January 1, with the Botanical Society of America, for the presentation of papers on mycology and plant pathology. The third session was held Wednesday afternoon, December 31, with the Botanical Society of America and the American Society for Horticultural Science. By invitation this last session was held at the Missouri Botanical Garden. A tour of inspection through the Garden and luncheon in the laboratory building preceded the program of invitation papers.

The annual dinner of the Society was held Tuesday evening, December 30, at the American Hotel Annex, and was attended by one hundred and seven phytopathologists and botanists. The dinner was followed by an extended discussion of the proposed Phytopathological Institute.

The following officers were elected:

President, Dr. Wm. A. Orton, United States Department of Agriculture, Washington, D. C.

Vice president, Dr. E. C. Stakman, University of Minnesota, University Farm, St. Paul, Minnesota.

Councilor for two years, Dr. G. H. Coons, Michigan Agricultural College, East Lansing, Michigan.

Members of editorial board: Editor elected for two years, Prof. H. S. Jackson, Purdue University, Lafayette, Indiana, and editor elected for three years, Dr. G. M. Reed, United States Department of Agriculture; associate editors for three years, Dr. N. J. Giddings, University of West Virginia, Morgantown, W. Va.; Dr. Neil E. Stevens, United States Department of Agriculture, Washington, D. C.; Dr. G. H. Coons, Michigan Agricultural College, East Lansing, Mich.; and Dr. Perley Spaulding, United States Department of Agriculture, Washington, D. C.; and business

manager elected for one year, Dr. G. R. Lyman, United States Department of Agriculture, Washington, D. C.

Member of the Editorial Committee of the American Journal of Botany for three years, Dr. C. L. Shear, United States Department of Agriculture, Washington, D. C.

The Society voted to hold its next annual meeting at Chicago, Ill., in conjunction with the American Association for the Advancement of Science, December 27, 1920, to January 1, 1921, inclusive.

AMENDMENT TO THE CONSTITUTION

The following amendment to the constitution, which was proposed at the Baltimore meeting, was adopted: After the words "two years" in the fourth line of the second paragraph of Article V there shall be added *and one member elected annually by each division*, making the paragraph read: The Council shall consist of the president, vice president, secretary-treasurer, the retiring president, and the chairman of the Board of Editors of the journal of the Society, with two members elected, one each year, who shall serve for a term of two years, and one member elected annually by each division.

REPORTS OF COMMITTEES

The Committee on Ways and Means made no formal report. It recommended, however, that its duties be delegated to the Advisory Board and the Committee discharged, and on motion this was done.

The Committee on Standards and Methods reported through its chairman that it had held two meetings and that tentative recommendations along certain lines would be ready for submission to members of the Society during the year. The Committee hopes that these preliminary recommendations will be carefully considered by the members and that action on them can be taken at the next annual meeting. On motion the report was accepted and the committee continued.

The Committee on Standard Chart for Percentage Estimates of Injury to Diseased Plants reported that it finds the chart now in general use by the Office of Cereal Pathology, United States Department of Agriculture, best adapted for most phytopathological purposes. It therefore brings this chart to the attention of the Society and recommends it as worthy of more general use. On motion the report was accepted and the committee discharged.

The Committee on Continuation of Extension and Investigational Emergency Work of the Department of Agriculture reported that it visited Washington after the Baltimore meeting and interviewed officials of the Department of Agriculture and Members of Congress, and that it was found impossible to secure continuation of the work desired. On motion the report was accepted and the committee discharged.

REPORT OF THE ADVISORY BOARD

The Advisory Board of American Plant Pathologists reported through its chairman, Dr. G. R. Lyman, on the work of the year. The report showed material progress in all lines of activity assigned to the Board by vote of the Society at the Baltimore meeting.

The Advisory Board has been accepted by the National Research Council as its Committee on Phytopathology, and the Chairman of the Board is serving as a mem-

ber of the executive committee of the Division of Biology and Agriculture of the Council. During the year a number of important matters were referred by the Council to the Board for advice, and this advisory function of the Board will increase in importance as the work of the Council develops. Through the Board the American Phytopathological Society will be constantly in close touch with the work of the Council and matters of phytopathological interest can be brought immediately to the attention of the Council at any time. The Council has also assisted the Board financially.

A list of the active phytopathological projects in progress in the country for 1919 was prepared and distributed by the Board, and it is felt that a fairly general response was made to this the first request for information of this kind. The list for 1920 will be prepared in coöperation with the Division of Research Information of the Council and should be more complete and valuable than the list for 1919.

During the year three important conferences of workers were held. The first of these was a conference of pathologists, horticulturists, botanists, and growers interested in problems relating to the growing, storage, and marketing of sweet potatoes, and in the diseases of southern crops, such as cotton, corn, and tomatoes. This was called by Prof. H. W. Barre, commissioner for the southern section, and held at Birmingham, Ala., February 26–28, 1919, in connection with the annual meeting of the Association of Southern Agricultural Workers. Forty-six persons, representing thirteen States and the United States Department of Agriculture, were in attendance. After full discussion of all phases of the general sweet-potato problem specific recommendations for future coöperation were adopted, and a committee of three, Prof. H. W. Barre, of Clemson College Agricultural Experiment Station, Prof. G. C. Starcher, Horticulturist at the Alabama Polytechnic Institute, and R. G. Hill, of the Bureau of Markets, United States Department of Agriculture, was appointed to assume leadership in this work. During the year material progress was made and a second conference will be held in connection with the next meeting of the Association of Southern Agricultural Workers in February, 1920.

The second conference was held at Portland, Oregon, April 23 and 24, 1919, under the leadership of Prof. H. P. Barss, Commissioner for the West, on pine-blister rust. This gathering was attended by pathologists, foresters, lumbermen, timber owners, quarantine officials, and others interested in the preservation of the western white-pine industry, and was very important, inasmuch as it was the first occasion on which all those interested in western white pine and its preservation from the blister rust met for consideration of their common problems.

The third meeting was a field meeting held on Long Island June 24–28, 1919, for the consideration of potato diseases, with particular reference to leaf roll and mosaic. The purposes of this conference were to get together as many potato pathologists as possible in a field meeting where informal discussion would be held; to have associated with them in the conference entomologists, agronomists, horticulturists, and others interested in the pathological problems of the potato; to secure international interest through the attendance of foreign plant pathologists; and to promote further coöperative work on potato diseases. About one hundred persons were in attendance. The success of the meeting was due largely to the committee on arrangements, consisting of Prof. M. F. Barrus, and Messrs. W. A. Orton, E. J. Wortley, Paul A. Murphy, and C. R. Orton. Many special plantings and field tests had been arranged in anticipation of the conference.

Not only was the meeting of great importance in securing a wider knowledge of and interest in certain potato diseases, but the occasion was notable because of the

presence of five representatives from foreign countries. Besides Mr. E. J. Wortley, Director of Agriculture, Bermuda, and Mr. Paul A. Murphy, Pathologist, Dominion of Canada, three distinguished potato pathologists from Europe were in attendance: Dr. A. D. Cotton, Mycologist of the Board of Agriculture, England; Dr. George H. Pethybridge, of the Board of Agriculture, Ireland; and Dr. H. M. Quanjer, of the Pathological Laboratory, Wageningen, Holland. The presence of these foreign pathologists, who spent some time in this country following the Long Island meeting, proved a great stimulus to all those who were so fortunate as to meet them. The Advisory Board hopes to secure the attendance of other foreign pathologists on the occasion of future meetings.

During the year progress was made on certain coöperative projects, among the most active of which were those on potato seed treatment under the leadership of Dr. I. E. Melhus, and on potato spraying, under the leadership of Prof. G. R. Bisby.

Among the other activities of the Advisory Board the most important was the consideration of the proposed Phytopathological Institute. This project was first brought to the attention of the Board by resolutions adopted by the cereal pathologists at St. Louis in June, 1919. The Board has been considering the nature of such an institute and learning the sentiment of American plant pathologists, and has secured the active interest and coöperation of the National Research Council. The matter has now reached the point where it must receive the careful consideration of the American Phytopathological Society. It was discussed at the annual dinner of the phytopathologists.

The Board reports with great regret the resignation of Mr. Paul A. Murphy as commissioner for Canada, due to his approaching departure from America to pursue pathological work in Ireland with Doctor Pethybridge. Mr. Murphy has been a most active and valuable member of the Advisory Board and his loss will be felt by all American pathologists.

REPORT OF THE TREASURER, 1919

Receipts:

Balance from 1918	$370.04	
Members dues	2,355.00	
Exchange	1.52	
Interest	23.57	$2,750.13

Expenditures:

Member subscriptions transferred to PHYTOPATHOLOGY	$1,178.00	
Clerical assistance	135.15	
Postage and supplies	32.30	
Traveling expenses of secretary to annual meeting	11.29	
Printing and stationery	124.79	
Annual appropriation to PHYTOPATHOLOGY	200.00	$1,681.53
Balance		$1,068.60
Balance due sinking fund from 1918	315.58	
Amount due sinking fund from 1919	445.00	760.58
Actual balance		$308.02

During the year a membership drive, organized by the secretary-treasurer, with the coöperation of members of the Society in the various States and in Canada, yielded a large measure of success. Eighty-four persons were nominated during

the year for membership and paid their dues for 1919 and their names were placed on the mailing list for PHYTOPATHOLOGY. The formal election of these candidates is necessary at this meeting. In addition sixty others have been proposed for membership beginning with 1920. This makes a total of one hundred and forty-four new members to be elected at this meeting. Sixteen members were suspended this year for non-payment of dues, and there were four deaths and two resignations. Deducting this loss of twenty-two we have a net gain of one hundred and twenty-two, which brings our total membership up to five hundred and twelve. Of this total five are full-paid life sustaining members, eighty-two are life sustaining members paying currently, and four hundred and twenty-five are regular members. Without doubt further large additions can be made to our membership list and each member of the Society is urged to continue his efforts to add new names during the year 1920.

FINANCIAL STATEMENT OF THE BUSINESS MANAGER OF PHYTOPATHOLOGY, 1919

Receipts:

Balance from 1918	$451.99	
Subscriptions and sales	1,479.85	
Wortley for illustrations in PHYTOPATHOLOGY	15.00	
Appropriation from American Phytopathological Society	200.00	
Gift from M. L. Delafield	50.00	
Advertising, 1918	193.28	
Member subscriptions	1,178.00	
Interest on sinking fund	60.00	
Sale of single copy of No. 4, Vol. VIII	.85	$3,628.97

Expenditures:

Manufacture of journal:			
No. 10, Vol. VIII	$259.16		
No. 11, Vol. VIII	159.73		
No. 12, Vol. VIII	321.10		
No. 1, Vol. IX	314.78		
No. 2, Vol. IX	375.91		
No. 3, Vol. IX	240.05		
No. 4, Vol. IX	193.26		
No. 5, Vol. IX	202.45		
No. 6, Vol. IX	327.18		
No. 7, Vol. IX	221.57		
No. 8, Vol. IX	241.31	$2,856.50	
Miscellaneous bills, Williams & Wilkins Co		173.78	
Insurance		5.40	
Clerical work		41.17	$3,076.85
Balance			$552.12

During 1918 a volume of 627 pages was issued. During 1919, notwithstanding an increase of approximately 29 per cent in cost of printing, a volume of 587 pages was issued. We face a still further increase of about 22 per cent in cost of producing PHYTOPATHOLOGY in 1920, which necessitates a further and considerable reduction in the number of pages for Volume X. The rapidly increasing cost of manufacturing the journal must receive the very careful consideration of the Council.

An auditing committee, consisting of C. W. Edgerton and F. D. Fromme, was appointed to examine the accounts of the treasurer and business manager. This committee reported the accounts correct and the reports were adopted.

RESOLUTIONS

A Committee on Resolutions regarding deceased members was appointed by the president. This committee, consisting of Donald Reddick and E. A. Bessey, offered the following resolution, which was unanimously adopted by a rising vote: "Within the past year there have passed from among us the following members of our Society: Samuel M. Bain, A. T. Bell, William Gilson Farlow, and Kenneth B. Laird. The Society assembled in annual convention places on record its sincere regret at the passing of these faithful and earnest colleagues, and with sorrow inscribes on its minutes this expression of its esteem for associates removed from our midst."

MISCELLANEOUS BUSINESS

The secretary's report of the tenth annual meeting, at Baltimore, as published in No. 4, Volume IX of PHYTOPATHOLOGY, was adopted without correction.

The Society voted to appropriate from any of its available funds the sum of two hundred dollars for the use of PHYTOPATHOLOGY in 1920.

On recommendation of the Council it was voted that two members at large be added to the Advisory Board of American Plant Pathologists, and it was also recommended that the Advisory Board organize with an executive sub-committee to facilitate more frequent meetings for consideration of important business, especially that relating to the activities of the National Research Council.

It was voted unanimously that the American Phytopathological Society endorse most heartily the action of Section G in recommending to the American Association for the Advancement of Science the continued financial support of Botanical Abstracts.

By vote of the Society the secretary was requested to add to future nomination blanks space for the nomination of representatives of the American Phytopathological Society on the Board of Control of Botanical Abstracts.

The consideration of the establishment of a Phytopathological Institute, begun at the Phytopathologists' dinner, was continued by the Society, and, after discussion, the following resolutions, passed at the dinner, were unanimously adopted:

"*Resolved*, That the time has come when the importance of the work of phytopathologists fully justifies the establishment of a Phytopathological Institute—an Institute for the promotion of fundamental research in the broader field of phytopathology and for the stimulation of such research in educational and research institutions and among the members of the phytopathological profession both in this country and abroad.

"*Resolved*, That the American Phytopathological Society authorize the Executive Council, in conjunction with the Advisory Board of this Society, to proceed with full power by the appointment of special committees and by such other procedure as may be necessary to the realization of the establishment of a Phytopathological Institute."

During the discussion following the session devoted to the consideration of the topic Eradication of Plant Diseases the following resolutions were adopted.

"*Resolved*, That the Advisory Board foster vigorously eradication as a means of disease control by bringing together for mutual consideration all interested parties as growers, transportation companies, merchants, consumers, farmers, and public officials.

"*Resolved*, That the Society believes that this movement can best be served by a more active and better supported plant disease survey of the United States Department of Agriculture in coöperation with the States."

The serious congestion of the program, due to the large number of papers presented, was discussed. While this condition was recognized as a sign of healthy growth and activity, some measure of relief is necessary. On motion the matter was referred to the Council for action.

It was unanimously voted—

"That the Society heartily approves the efforts of the Advisory Board to promote and correlate coöperative experimental work; that the members of the Society pledge themselves actively and vigorously to prosecute the projects now under way insofar as time and funds permit; that the Society urge that the Board canvass the membership to ascertain which other lines of work should be inaugurated and pursued coöperatively; that it is the sense of the meeting that coöperation on potato seed certification, spraying, and dusting fruits, and other similar problems be organized immediately."

On motion the Chair appointed G. R. Lyman, Donald Reddick, and C. L. Shear a committee to codify the working rules of the Society and to revise the constitution in accordance therewith, the revision to be submitted to the Society for adoption at the next annual meeting.

The following resolution was unanimously adopted:

"The American Phytopathological Society, assembled in annual meeting at St. Louis on January 2, 1920, by unanimous vote desires to extend to the Society of Economic Entomologists and to Mr. E. D. Ball in particular an appreciation of the progress made in the investigation of leaf-hopper injury to potato, and further desires to express regret that through inadvertence in arrangements we as a body failed to hear the discussion of the Entomologists on this subject."

The Secretary was requested to send a telegram of greetings to Dr. Wm. A. Orton, president-elect of the Society, who was unable to attend the meeting. He was also requested to convey the appreciation of the Society to the manager of the Marquette Hotel, to the local committee on arrangements, and to the Missouri Botanical Garden and others for the accommodations provided for the Society and the many courtesies extended during the meeting.

ACTION OF THE COUNCIL

The Council reported the following action for the information of members of the Society:

PHYTOPATHOLOGY. The rapidly increasing cost of manufacturing PHYTOPATHOLOGY presents a problem of grave importance. A careful estimate of the resources of the journal for the year 1920 indicates that it will probably be possible to issue a volume of approximately 450 pages, notwithstanding the increased printing charges. In view of this fact the Council does not think it expedient to take steps at this time to raise membership dues. Moreover there is hope of financial assistance through the Division of Biology and Agriculture of the National Research Council, as this Division is endeavoring to assist biological publications. The interests

of PHYTOPATHOLOGY will continue to receive careful attention on the part of the Council, with a view to taking such action as future circumstances may render advisable.

Because of the rapidly decreasing stock of back volumes of PHYTOPATHOLOGY the price of such volumes was raised from five to six dollars, and the price for single numbers, when such can be sold without breaking a complete volume, was raised to one dollar where there were six issues per volume, and was fixed at 50 cents where there are twelve issues per volume.

Advisory Board. The Council selected Prof. A. H. Reginald Buller, of the University of Manitoba, to succeed Mr. Paul A. Murphy as commissioner for Canada. Prof. H. P. Barss and Prof. H. W. Barre were reappointed to succeed themselves as commissioners for the West and the South, respectively. The Council selected Dr. L. R. Jones and Dr. E. M. Freeman as commissioners at large.

Phytopathological Institute. In conjunction with the Advisory Board the Council considered further steps looking to the establishment of a Phytopathological Institute. Dr. E. M. Freeman was selected as leader in securing funds. All members of the Society are requested to consider themselves as members of this finance committee and to send Doctor Freeman suggestions as to sources of financial support or regarding the nature and work of such an institute.

Program of the annual meeting. In accordance with the vote of the Society the Council considered the problem of relieving the congestion of the annual program. It was not deemed expedient to extend the length of the session beyond four days, nor was it considered advisable at this time to run simultaneous sessions. The secretary of the Society was requested to send out the call for titles and abstracts in the future in time to permit the printing and distribution of the abstracts, together with the program, in advance of the annual meeting. It was suggested that the titles be grouped as far as possible according to the subject matter, one subject or group of subjects being assigned to each session. If the abstracts are prepared with sufficient care it was thought that in the future the entire time of the session can be devoted to discussion. The Advisory Board was requested to assist the secretary in working out the details of the program in accordance with these suggestions.

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